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**BIOLOGICAL PROCESSES
IN TROPICAL SOILS**

A. STEVEN CORBET

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BIOLOGICAL PROCESSES
IN TROPICAL SOILS

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PRIMEVAL FOREST AT GINTING SIMPAH.

BIOLOGICAL PROCESSES IN TROPICAL SOILS

with special reference to Malaysia

By

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TO MY PARENTS

The prosperity of the human race depends, in the last analysis, upon the soil. We ought to know just what is occurring in the various soils of the world.—

PROFESSOR E. M. EAST.

I could not help thinking that if rubber planters were not so anxious to get a large area cleared at once, it would probably pay better in the end to leave all the poorer patches of land in forest as a shelter to the rubber (*Hevea*).—

H. J. ELWES.

PREFACE

It is, perhaps, not sufficiently recognized that sweeping generalizations cannot be made upon so wide a theme as tropical agriculture. Within the tropics is included such a great diversity of climatic conditions that the problems and their solutions affecting one region may have no bearing upon those of another. The author, therefore, has applied the observations in this book to the special geographical sub-region of which he has the most intimate knowledge. Climatic conditions throughout the hot, wet equatorial belt, however, are so similar that the reader in other such regions should find much that is applicable to his own problems, provided that he makes due allowance for the variations in flora and fauna which are such vital factors in determining and in solving the problems of the soil biologist.

The following statements are borne out by such a mass of practical evidence that there seems to be little doubt of their validity.

- (a) A re-statement of Jenny's law to the effect that the nitrogen and organic matter content of the soil varies inversely with the soil temperature and the amount of solar radiation received.
- (b) At temperatures below 25° C. there is an accumulation of organic matter in the soil but, at temperatures above this, humus decomposition outpaces its formation.¹

When these tenets are accepted the whole process of formation and decomposition of soil organic matter in the humid tropics becomes clear. A practical agriculturist would find confirmation of these views on every hand yet, although the writer has shown in the laboratory that, under certain conditions, soils can lose nitrogen as a result of irradiation by ultraviolet light, the difficulty arises that, as far as can

¹ It is, of course, evident that, to a certain extent, (a) is a consequence of (b): see Fig. 8 on page 100.

be tested in the laboratory, ultraviolet light does not penetrate far below the soil surface. It may be concluded that the photochemical processes in soils are purely surface phenomena but many established facts are at variance with such a view.

After filtration by the earth's atmosphere, the solar spectrum comprises light of wave lengths between 30,000 and 2900 Angström units¹: the ultraviolet region consists of light of wave length below 4000 Å. and it is the radiations between 3100 and 2900 Å. which effect the greatest chemical activity.

At present, the practical course seems to be to accept the statements (a) and (b) given above as a working hypothesis, awaiting results of further research by those in a position to carry out such work.

A considerable volume of research work on the chemistry and microbiology of soils in temperate regions has been carried out during the past fifty years and among the institutions responsible for the advances made may be mentioned particularly the Rothamsted Experimental Station in England, under the direction of Sir E. John Russell, and the New Jersey Agricultural Experiment Stations with Drs. J. G. Lipman and S. A. Waksman. Important work has been done also in Germany, France, Holland, Hungary and other European countries. On the other hand, little progress has been made towards elucidating the problems peculiar to tropical soils; in fact, it is perhaps only within the last decade that any fundamental distinction has been recognized between the processes of temperate and those of tropical soils. The experimental work and field observations responsible for many of the conclusions elaborated in this book were carried out at the Rubber Research Institute of Malaya and are described in a series of papers entitled "Studies on Tropical Soil Microbiology," appearing in *Soil Science*.

This book was written primarily for agricultural chemists working in tropical countries, but it is hoped that planters, foresters and others may find it intelligible and useful.

¹ An Angström unit (Å.) = $1/100,000,000$ cm. = 10^{-8} cm.

It is, perhaps, as well to point out that the author has, of necessity, viewed the subject largely from the standpoint of the cultivation of a perennial crop, namely rubber. It may be suggested that some of the matter included is to be found in standard text-books: this is so because many well known works of reference are not always to be found in tropical laboratories. For this reason it has been thought advisable to include standard methods of soil analysis in the appendix.

August, 1934.

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A. S. C.



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LIMESTONE OUTCROP IN SELANGOR.

I. MALAYSIA

THE countless ages that have elapsed since the earth reached its present form have witnessed many profound changes, both geographical and climatic. Malaysia has not always been the forest-covered group of tropical islands that we know to-day, and, in order to form a proper appreciation of present conditions, it is necessary to give at least a cursory glance at some of the outstanding events which have taken place in the past. However, although the geological record of western Europe is known in some considerable detail, much of the former history of south-east Asia is shrouded in obscurity.

Geological time is divided into a number of *eras* (Fig. 1): although life dawned in the earliest of these, the Eozoic era, the formation of the earth antedates the first appearance of organic life by millions of years. As far as the record of the rocks shows, the oldest fossils are sponges but other organisms also existed in pre-Cambrian times.

During the Primary era the lands which now constitute south-east Asia were at the bottom of the ocean but events of considerable importance were taking place in other parts of the world. It was in the Cambrian age that living organisms first occurred in numbers, although at this time they were entirely marine; the crustacean-like trilobites, whose nearest living allies are the king-crabs (*Xiphosura*), were characteristic of this period. By the Devonian age the trilobites had been eclipsed and fishes represented the highest achievement of creation; vegetation had appeared on the land, but the flora was largely composed of conifers, tree ferns and club mosses. A ghostly silence must have pervaded the land for few terrestrial creatures existed, no birds, and few insects save cockroaches, for still almost the entire animal world was marine in habitat. Insects began to appear in numbers at the close of the Primary era but few of them would appear familiar to an entomologist to-day.

It appears that Malaysia had its beginnings in the Secondary era, probably as a consequence of the intense

volcanic activity in some of the eastern parts of the continent of Gondwanaland, which stretched across the Indian Ocean to Africa at least. It was during the Jurassic age that the monstrous reptiles, such as the flying Pterodactyl, the

EOZOIC ERA	
PRIMARY ERA	Cambrian Age Ordovician Age Silurian Age Devonian Age Carboniferous Age Permian Age
SECONDARY ERA	Triassic Age Jurassic Age Cretaceous Age
TERTIARY ERA	Eocene Age Oligocene Age Miocene Age Pliocene Age
QUATERNARY ERA	Pleistocene Age Holocene Age

FIG. 1. TABLE OF GEOLOGICAL AGES.

In a general way, it may be said that existing *species* first appeared in Pliocene times, existing *genera* appeared in the Miocene age, existing *families* were found in Oligocene times, while existing *orders* date from the Eocene age. Man first appeared in late Pliocene times.

predacious Tyrannosaurus and the herbivorous Atlantosaurus (over seventy feet in length), were masters of the earth. These creatures occurred in Britain, and in fact all over the world, but they probably became extinct before Malaysia was in a habitable condition.

By the time of the Eocene age, which ushered in the Tertiary era, the forms of life prevailing were not vastly different from those existing to-day. Mammals first appeared in the Secondary era but they made little progress

in development or numbers until Eocene times; birds were represented by an ever-increasing number of species, but the age of giant reptiles was deep in the past, and such creatures as the Iguanodon now slept in a grave of chalk. Then, and during the successive Oligocene and Miocene ages, the climate of western Europe was subtropical and supported a rich flora and fauna; there was still a tremendous amount of volcanic activity in south-east Asia and, somewhere about this time, the mighty Himalayas came into being.

At the close of the Pliocene age many animals, such as antelopes, apes and elephants which still exist in tropical regions of the world at the present time, roamed western Europe and man had already appeared and walked erect. In these times, comparatively little remote from the present, where to-day in south-east Asia exists a number of islands, was a unified land mass known as SUNDALAND. This land lay between the parallels of 10° N. and 13° S. and between longitudes 94° and 120° E.: the general trend of the mountain ranges was east and west; many of the rivers were probably long and characterized by wide mouths, the climate was uniformly warm and humid and the plains and mountain slopes were covered with dense forest. In fact, except for the difference in the area of land there is no reason for supposing that, at the close of the Tertiary period, Sundaland differed in any remarkable way from this region to-day. The plants and animals found on Sundaland largely comprised those occurring in the Malay Peninsula, Sumatra, Borneo and Java at present.

But in western Europe the Pliocene age was marked by a progressive cooling until most of Britain was covered with a permanent mantle of snow and the Ice age set in; the flora and fauna characteristic of tropical and subtropical regions disappeared and were replaced by organisms adapted to colder climates. It is probable that at this time there was a lowering of temperature over the whole of the earth's surface although it is unlikely that any appreciable cooling took place in south-east Asia where there was still much volcanic disturbance. But, contemporaneously, geological

movements were taking place in Sundaland which culminated in its disintegration into a number of islands. Geological evidence indicates that there was a number of upheavals and subsidences, not necessarily of a violent character, which effected alterations in the level of the land: most of the changes known to have taken place can be accounted for by the gradual sinking of the land level by

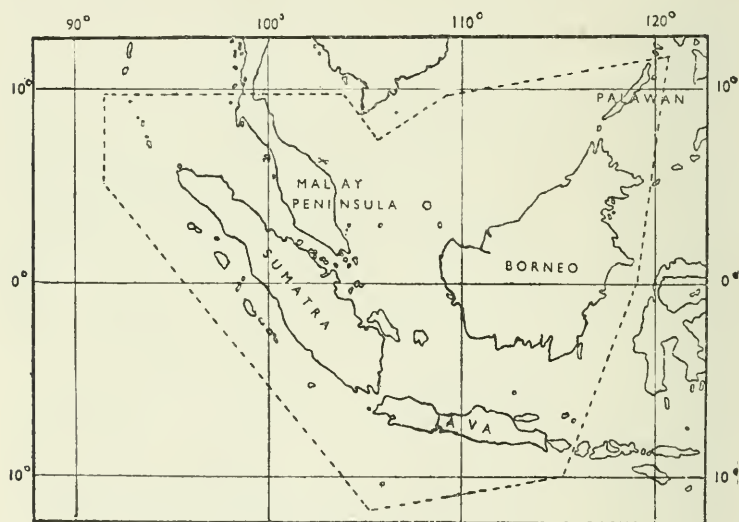


FIG. 2. MALAYSIA.

a few feet. Of what are termed the Large Sunda Islands,¹ it is evident that Java was the first to be cut off, then later, probably much later, occurred the isolation of Borneo, followed closely by the separation of the present Malay Peninsula from Sumatra.

The wide plains of the ancient continent of Sundaland now form a continental shelf varying from 50 to 100 fathoms in depth below sea level: in fact, a steamer can anchor almost anywhere on the *Sunda shelf*. What were foothills or elevated plateaus are now the green coastal plains of the Malay Peninsula and the Sunda islands: the mountains of Sundaland

¹ The superscript numerals refer to references at the end of the chapter.

are still the forest-clad heights which sweep in a wide curve through the whole region.

What remains of Sundaland above sea level to-day is termed MALAYSIA and this includes the Malay Peninsula south of latitude 10° N., the Large Sunda Islands (Sumatra, Borneo and Java), Bali, almost certainly Palawan and Balabac, and innumerable lesser islands situated in the vicinity. The deep sea islands off the west coast of Sumatra (Engano and the Mentawai Islands), Christmas and Cocos-Keeling Islands, and possibly the Nicobar Islands also, are to be regarded as part of Malaysia, although it is certain that Christmas and Cocos-Keeling Islands were never united with the mainland.² The *Malay Archipelago* is usually regarded as comprising the Malay Peninsula and all the islands forming a chain from Sumatra to New Guinea. The term *Malaya* is now restricted to that part of the Peninsula under British control or protection and, although there may be certain objections to its use, it is now pretty generally employed. Strictly speaking, the Malay Peninsula extends from the Isthmus of Kra to Cape Roumania in Johore.

Beyond the Sunda shelf considerable depths are soon reached, particularly in an easterly direction where the ocean bed drops to some 3000 fathoms.

The history of the land connection between Sundaland and the mainland of Asia is of interest. Biological evidence (p. 27) suggests that the Sunda mountains were linked with the Himalayan range at some remote date; but it is clear that at no very distant time the present Malay Peninsula was cut off from the mainland of Asia by the sea. The flora and fauna show that Malaya was separated from Siam and south Burma in south Kedah, the boundary being the Kedah river: as far as the geological evidence goes, it supports this conclusion, which also finds confirmation in early tradition.³

It is of particular interest to note that the remains of one of the earliest known men, *Pithecanthropus erectus*, were found in Pleistocene deposits in Java in 1891-92. It is possible that the negrito peoples of Malaysia (Semang

of the Malay Peninsula, Kubus of Sumatra, Aita of Palawan and possibly the Andaman Islanders) occupied Sundaland while it was still one large land mass.

Sumatra and Borneo are intersected by the equator, Java lies to the south of it and the Malay Peninsula to the north. In all these countries the geological formation, climate, flora and fauna are similar, and, in the natural state, the land is covered with dense primeval forest. With the exception of Java, all these lands still retain most of the original jungle and on this account they are of particular interest to the biologist and bacteriologist. The former has the opportunity of investigating the flora and fauna of a natural region as yet unspoilt by civilization while the latter has the advantage of studying the activities of micro-organisms with two important factors, temperature and humidity, maintained at a constant level. Other reasons that render Malaysia of peculiar interest to the soil micro-biologist will become apparent later on.

THE MALAY PENINSULA

The Malay Peninsula is usually regarded as extending from approximately 1° N. to the Isthmus of Kra, 10° N. but British Malaya does not reach 7° N. and the total area under British control or protection is about 51,000 square miles. The peninsula is formed of strata of Primary and Secondary origin and the geology has been investigated in some detail.⁴ The greater proportion of the rocks consists of granite and, to a lesser extent, quartzite but there are numerous outcrops of other formations such as gneiss, schist and marble. Sedentary deposits include slate, limestone and sandstone: coal occurs at Rawang and in one or two other small areas of Tertiary rocks. On the west coast there are several limestone bluffs, particularly in the neighbourhood of Kuala Lumpur, and in Perak, Kedah and Perlis.

Running through the centre of the Peninsula is a range of granite mountains: this range is more or less continuous from north Johore to Peninsular Siam although it is interrupted at the point where, it is believed, the Peninsula

was formerly separated from the mainland of Asia. In addition to the main range are a few smaller parallel chains, of which the most important are the Larut Hills in Perak and two or three ranges in Pahang. In general the main range attains a height of some 4000 feet, although it is broken by numerous peaks of which the highest is Gunong Kerbau (7160 feet): the highest mountain in the Peninsula is Gunong Tahan (7186 feet) on the Pahang-Kelantan border. There are no extensive plateaus in the mountains such as occur in Sumatra but a large raised valley near the Perak-Pahang border, known as Cameron Highlands, is being developed as a hill station.

Although Malaya possesses numerous rivers few of them are suitable for navigation by sizeable craft for any considerable portion of their length. In the upper part of their courses, all the rivers are swift and usually characterized by numerous cascades and rapids. The longest river, the Sungei Pahang, flowing into the China Sea on the east coast, is navigable for native craft for some 250 miles; the Sungei Kelantan, entering the China Sea further to the north, can be used for nearly the same distance. Of the rivers flowing into the Straits of Malacca on the west coast the most important are the Sungei Perak, the Sungei Bernam and the Sungei Muar: although shallow, the first-named is navigable by native craft for over 200 miles.

The coast line is fairly regular but, at the river mouths, the water is shallow. On the west coast, mangrove swamps persist for a depth of several miles, except in a few spots where sandy beaches occur. On the east coast mangrove forests are to be found only at the tidal estuaries, sandy beaches fringed with coconut palms and *Casuarina* trees being the rule. The formation of mangrove forests occurs in sheltered areas where the sea is shallow and quantities of silt are deposited in the neighbourhood of river mouths: the absence of such forests on the east coast of Malaya is attributable to the force of the north-east monsoon which blows from November to February.

Several islands lie off the coasts of the Peninsula; the largest being Pulau Langkawi in the group of Langkawi

Islands west of Kedah. Penang and Pangkor are other large islands off the west coast and Singapore Island is the chief member of the Rhio Archipelago. On the east coast, off Pahang and Johore are Pulau Tioman and Pulau Aor with some smaller islands, while the Perhentian Islands lie farther north.

In its primitive state the whole of the Malay Peninsula was covered with dense primeval forest and even to-day over seventy *per cent.* is forested. The only cultivated crops of any importance are rubber, coconuts and rice, and of these the first-named is by far the most outstanding. Some thirty *per cent.* of the world's tin is obtained from the Peninsula where it occurs as cassiterite and always close to granite: almost all the tin is alluvial but the lode mines at Sungei Lembing, near Kuantan, are the deepest tin mines in the world.

The population of British Malaya is over four millions. Three aboriginal races are found of which the oldest is the Semang, a tribe of negrito people with frizzy hair and of small stature who lead a nomadic existence in the forest and make no attempt at cultivation. The Semang are closely related to the negritic peoples found in the Andaman Islands, Sumatra and Palawan. Other pagan races found in Malaya are the Sakai and the rather similar Jakun. The modern Malays reached the Peninsula from Sumatra in comparatively recent times. Other nationalities constituting an appreciable proportion of the population are Chinese, Tamils and Europeans.

SUMATRA

The island of Sumatra has an area of some 167,000 square miles and is formed largely of strata of the Tertiary period, but contains a few formations anterior to this. A high mountain chain runs the length of the island parallel to the west coast: the mountains rise abruptly from the narrow coastal strip in the west but descend gradually to the wide plains in the east. This chain is a link in an archaic mountain system persisting to-day only in fragments in south Burma, the Andaman and Nicobar Islands, Sumatra, Java,

the Lesser Sunda Islands and the Moluccas. In both Sumatra and Java are numerous volcanic peaks, many of which are still active.

The loftiest peak in Sumatra is Korinchi (12,484 feet), also known as Indrapura, and there are several summits in the neighbourhood of 10,000 feet. As would be anticipated from the geographical configuration of the island, the rivers on the west side of the main range are short, flowing in deep valleys, while those on the east are longer and slower: the east coast is fringed with mangrove swamps and many of the estuaries are constantly changing position. The most important river in Sumatra is the Asahan, which drains into Toba Meer, a large lake some forty-five miles long and fifteen miles broad, situated in the Battak mountains. In the centre of this lake is an island, Pulau Samosir; the greatest depth of the lake is about 1460 feet. Other important rivers are the Panei, Rokan, Kampar, Indragiri and Jambi: the last-named, which is the largest river in Sumatra, rises in Mount Korinchi and is navigable for some five hundred miles.

In some regions of the highlands of Sumatra, particularly in parts of the Battak Plateau, lying more than 2000 feet above sea level, are large areas of savannah country covered with lalang (see page 30); on such areas little or nothing else will grow.

The population of Sumatra is about six millions. The oldest race, the Kubus of the Jambi Mountains, are of negritic blood and small stature; they lead a nomadic existence in the forests. Of the Malay races which constitute the rest of the indigenous population, the Achinese occupy Achin in the north-west of the island, further south are the Gayos, and the Battaks are found in the Battak Plateau and in the mountains around Toba Meer. The Menangkabau Malays of the Padang Highlands still retain matriarchal law. Other Sumatran races of lesser importance found in the southern portions of the island are the Korinchis, Rejangs and the Jambi Malays.

The most important agricultural crops are tobacco and rubber, but timber and gums are products also of

consequence. Coal and petroleum occur in some quantity and the adjacent islands of Banka and Billiton have long been famed for the production of tin.

JAVA

Together with the island of Madura, Java has an area of about 51,000 square miles of which about forty *per cent.* of the total is under cultivation. The whole island is covered by deposits of the Tertiary and Quaternary ages, and is the most actively volcanic region in the world, over a quarter of the total area of the island being covered with volcanic rocks.

The mountain range, running east and west, follows on the course of the main chain of Sumatra, and although the area of mountainous country is not nearly as extensive as is the case in the rest of Malaysia, there are several peaks above 9000 feet. The highest mountain in Java is Gunong Semero (12,300 feet). The rivers are of little importance: the Chi Tarum and the Chi Manuk flow into the sea on the north coast while the Chi Tanduwi enters the sea on the south. The north coast of the island is covered with nipah and mangrove areas, sandy stretches and shifting river mouths.

Relative to the rest of Malaysia, the population of Java is enormous. The total population is in the neighbourhood of thirty-six millions; thirty-five millions belong to the Malay races, the most important of which are the Javanese proper, the Sundanese and Madurese.

Rubber, rice and sugar are the most important crops in Java, but a large number of other products are cultivated, including coffee, tea, tobacco, copra, cinchona, indigo, spices and teak. The island is poor in metallic ores.

BORNEO

The island of Borneo (politically divisible into Dutch Borneo, Sarawak, British North Borneo and Brunei) has a total area of nearly 300,000 square miles and ranks after Greenland and Papua as the third largest island in the world.



NIPA FRUTICANS.

The geology of Borneo has not yet been investigated in any detail; there appears to be a preponderance of rocks of Tertiary and Quaternary origin but a number of fossils have been found in some Secondary deposits.

Borneo is a mountainous country although no range attains any great elevation. The mountain ranges radiate from an approximately central point, the Iran Mountains running to the north, the Upper Kapuas chain to the west, the Madei and Schwaner Mountains to the south-west and the rather low Batu Tapatung range to the east. The highest peak in Borneo, and in fact in the whole of Malaysia, is Mount Kinabalu (13,455 feet) situated in the north of British North Borneo: this peak is of considerable interest on account of its specialized flora and fauna.⁵ The next highest Bornean mountain is Mount Mulu (9600 feet) in north Sarawak.

A number of rivers in Borneo attain a considerable length: the Rejang in Sarawak flows into the South China Sea, and steamers can ascend this river for one hundred and fifty miles, while the river is navigable for native craft for five hundred miles. Other important rivers are the Kina-batangan in British North Borneo, the Kapuas which enters the sea on the west coast in Dutch Borneo and the Barito and Kutai flowing into the Java Sea and Macassar Strait respectively on the east. For the most part the coast line of Borneo consists of low alluvial lands, broken by occasional sandy stretches fringed by *Casuarina* trees, while in the neighbourhood of river mouths are mangrove and nipah swamps.

The population of Borneo is about three millions. No negritic races are known and it is improbable that any remain. The indigenous population is Malayan and a great deal of intermixture appears to have taken place in recent times among the various races. Roughly, the Malayan races of Borneo can be divided into the Laut and the Dyaks; as the names imply, the first of these comprises the peoples living on the sea coasts while the latter are Mohammedans living in the interior. In British North Borneo the Dusuns, Bajans and Muruts constitute the most important tribes.

The country is but little developed: rubber, sago and timber are the principal agricultural products and coal and petroleum are becoming increasingly important; metallic ores are scarce.

BALI

Besides the Larger Sunda Islands, Malaysia includes innumerable smaller islands, the largest of which are Bali and Palawan. Bali has an area of 2000 square miles and is mountainous, the highest peak being the volcanic Mount Agung (10,500 feet). Many devout Hindus fled to Bali from Java when the Arabs visited the latter island in the sixteenth century and employed coercive measures to convert the inhabitants to their belief; and the Balinese are still adherents to the Hindu faith. The population of the island is in the neighbourhood of one million and the Balinese have the reputation of being expert rice growers.

PALAWAN

Politically one of the Philippines, Palawan (area 4500 square miles) appears to be more closely related faunistically to Malaysia than to Mindora. A mountain range between 4000 and 5000 feet in height extends through the island where a dwarf, negrito people, the Aita, still survive.

FAUNISTIC REGIONS

In the natural course of evolution one species of plant or animal gives rise to others which, in turn, are the precursors of further forms: each endeavours to extend its range of distribution as far as possible, but in most cases this can be effected only to a limited extent. A species of plant or animal on a remote oceanic island has but a slender chance of extending its range compared with one on a continental land mass. As a general rule, however, the geographical range of a species cannot be increased indefinitely because, sooner or later, the plant or animal in question arrives at a locality where climatic conditions are unsuitable for it, and it can penetrate further only if it is still in a plastic stage and able to adapt itself to meet the

altered conditions. Another reason for the abrupt conclusion of an advance into new territory, such as we have described, may be the meeting of some impassable barrier such as the sea, a desert or a high mountain range.

The existence of such barriers on the surface of the earth has resulted in the land area being divided into a number of well-defined faunistic regions, each of which has its own characteristic flora and fauna. While the passage from one region to another is not absolutely barred it appears that it took place very infrequently in the past but, owing to increased travelling facilities brought into being recently by man, transference of a species from one region to another is now by no means rare. There is no particular reason why a plant or animal from Brazil should not thrive in the eastern tropics once it has gained a footing; in fact it is surprising how frequently a plant or animal introduced from one region to another will multiply in the new area—often to the detriment of endemic species. In Table IV (page 32) are given the names of plants well known in Malaysia, many of which have been introduced within recent times from countries in other faunistic divisions.

The four faunistic regions of the world are: the *Palaearctic Region*, comprising Europe, Africa north of the Sahara Desert and that part of Asia lying north of a line drawn from Baluchistan, through the Himalayas and across China to Shanghai; the *INDO-AUSTRALIAN REGION*, comprising that part of Asia south of the Palaearctic region, the Malay Archipelago, Australia, New Zealand and the South Pacific Islands; the Hawaiian Islands properly belong to this region although they now contain a number of species of plants and animals introduced from America; the *Ethiopian Region*, constituting the continent of Africa south of the Sahara Desert; and the *American Region*, comprising the whole of the American continents. In the last-named region the transition from the tropical to the temperate zones is gradual and several tropical species extend far into the United States.

Considering the varied geographical and climatic nature of the Indo-Australian region (the division which concerns

us most closely), it is surprisingly homogeneous but admits of further division into a number of sub-regions, each of which shows greater uniformity. The MALAYSIAN SUB-REGION includes the Malay Peninsula, Sumatra, Borneo, Java, Bali, Palawan and the adjacent small islands—in fact, all that persists of the original Sundaland. It is a remarkable fact that even to-day, in most respects, the flora and fauna of Malaya are more closely allied to those of Sumatra than to those of south Burma, in spite of the gradual infiltration of species which must have been taking place for centuries. It might be anticipated that, with the passage of time, the flora and fauna of the Malay Peninsula would show less affinity with Sumatra and become more Burmese in character. This may be true but, probably, only within limits; for climatically the Malay Peninsula is an island and there are climatic factors operating which inhibit the establishment of certain Burmese elements in the Peninsula. In some respects the Langkawi Islands have more the faunistic characters of south Burma than of the Malay Peninsula. The Indian crow (*Corvus splendens*), so abundant in Burma, is very common on Pulau Langkawi, but, although increasing rapidly now, has made little headway since it was introduced into the Malay Peninsula some forty years ago. Several species of insects occurring in the Langkawi Islands are definitely of Burmese origin and do not otherwise extend into the Malaysian sub-region.

Introduced plants and animals usually have to contend with the native species and, although on occasion immigrants may be entirely successful in the struggle, cases must occur constantly where introduced species fail to become established in a new faunistic area.

It is certain that many of the islands which pertain to Malaysia were never connected with either the mainland of Asia or Malaysia. Such islands are termed *oceanic* in contrast to *continental* islands which originated as part of a large land mass. The remote Christmas Island, nearly two hundred miles south of Java, is an instance of a Malaysian oceanic island. This island, known for its phosphatic deposits, has a flora and fauna containing many distinct

forms, but all show a certain degree of affinity with species found in the Large Sunda Islands.⁶

CLIMATE

Malaysia lies in the equatorial belt of low pressure and the chief characteristics of its climate, therefore, are high temperature and humidity and heavy rainfall. The seasonal changes are slight and are determined by variations in rainfall and not in temperature.

The mean annual shade TEMPERATURE on the plains throughout Malaysia is in the neighbourhood of 80° F. and the range of variation between the monthly means is between 2° and 3° F. The mean temperature at Rangoon, in south Burma, is just under 80° F., but the range of variation is over 10°. In the primeval forest the temperature is somewhat lower: in the Malay Peninsula⁷ the temperature at the surface of the soil was found to be 77° F., and this value did not show a variation of more than 1° F. during the course of a year. As the hills are ascended the temperature falls, as is shown in Table I, which gives figures obtained

TABLE I
THE VARIATION IN TEMPERATURE WITH ALTITUDE IN JAVA

Altitude.		Mean temperature.		Minimum temperature.		Maximum temperature.	
Metres.	Feet.	°C.	°F.	°C.	°F.	°C.	°F.
0	0	26.5	79.7	22.0	71.6	33.0	91.4
200	650	25.0	77.0	20.0	68.0	30.0	86.0
1,000	3,280	20.0	68.0	15.0	59.0	25.0	77.0
1,800	5,900	15.0	59.0	10.0	50.0	20.0	68.0
2,600	8,530	10.0	50.0	5.0	41.0	15.0	59.0
3,400	11,150	5.0	41.0	0	32.0	10.0	50.0
4,300	14,100	0	32.0	(snow limit)			
and above.		and below.	and below.				

E. C. J. Mohr, *De Grond van Java en Sumatra* (Amsterdam), 1930, p. 11.

for Java: in general, throughout the world an increase in altitude of 300 feet is equivalent to a fall in the average temperature of 1° F. On the banks of Toba Meer in Sumatra,

at an altitude of 3770 feet, the mean temperature is 70° F. The mean monthly temperatures in certain Malaysian localities are given in Table II.

TABLE II
MEAN MONTHLY SHADE TEMPERATURES IN MALAYSIA
(Degrees Fahrenheit.)

	Penang (Malaya).	Singapore (Malaya).	Gunong Tahan (Malaya).	Padang (Sumatra).	Fort de Kock (Sumatra).	Batavia (Java).	Bandoeng (Java).	Pontianak (Borneo).	Sandakan (Borneo).	Christmas Island.
Altitude in feet.	23	10	5460	3	3500	23	2366	10	98	
January	80°	78°	60°	79°	69°	78°	72°	78°	79°	80°
February	80°	79°	61°	80°	69°	78°	72°	79°	80°	80°
March	81°	80°	62°	79°	70°	79°	72°	79°	81°	80°
April	82°	81°	63°	80°	70°	79°	72°	79°	81°	80°
May	82°	82°	64°	80°	71°	79°	72°	80°	82°	79°
June	81°	81°	65°	79°	70°	79°	72°	80°	81°	79°
July	80°	81°	64°	79°	69°	78°	72°	80°	81°	78°
August	80°	81°	63°	79°	69°	79°	72°	79°	81°	78°
September	80°	80°	63°	79°	69°	80°	72°	79°	81°	78°
October	80°	80°	62°	79°	70°	80°	73°	79°	81°	79°
November	79°	79°	62°	79°	69°	79°	72°	78°	80°	79°
December	79°	79°	60°	79°	69°	78°	72°	78°	79°	79°
Range	3°	3°	5°	1°	2°	2°	1°	2°	3°	3°
Mean annual temperature	80°	80°	62°	79°	69°	79°	72°	79°	80°	79°

The annual RAINFALL often differs very considerably in different localities as Table III shows; nevertheless, it may be stated that the rainfall of most places on the plains in Malaysia is in the neighbourhood of 100 inches per annum.

Of the meteorological stations in the Malay Peninsula, that at the "Cottage" (4500 feet) in the Taiping Hills has the heaviest rainfall—an average of 259 inches per annum (1912 to 1919), while Jelebu in Negri Sembilan has the lowest (60 inches per annum from 1905 to 1919). The west coast of Sumatra has an annual rainfall of 122 inches, the east coast 106 inches and the north coast 96 inches. The rainfall at Batavia is lower than at most places on the

plains of Java but an annual rainfall of over 270 inches has been recorded from Kranggan in the Javanese mountains: the rainfall in Borneo appears to be appreciably higher than in other parts of Malaysia.

The intensity of the rainfall in the tropics is often a factor of considerable importance for, very frequently, during a

TABLE III
MEAN MONTHLY RAINFALL IN MALAYSIA
(Inches.)

	Penang (Malaya).	Singapore (Malaya).	Gunong Tahan (Malaya).	Padang (Sumatra).	Fort de Kock (Sumatra).	Batavia (Java).	Bandoeng (Java).	Pontianak (Borneo).	Sandakan (Borneo).	Christmas Island.
Altitude in feet.	23	10	5460	3	3500	23	2366	10	98	
January	3.9	8.5	20.7	13.5	9.2	13.0	7.6	10.8	19.4	5.5
February	3.0	6.1	5.6	9.9	7.0	13.6	7.1	7.9	9.9	12.5
March	4.7	6.5	7.5	11.9	9.2	7.8	9.6	9.8	7.8	9.0
April	7.0	6.9	10.6	14.0	10.2	4.8	9.0	10.8	4.1	6.2
May	11.0	7.2	11.2	12.6	7.6	3.7	5.2	10.7	5.1	7.6
June	7.2	6.7	5.0	13.0	5.6	3.6	3.6	8.7	8.6	3.4
July	8.9	6.8	7.0	11.8	3.8	2.6	2.6	6.3	10.0	7.7
August	12.8	8.5	8.3	13.7	6.4	1.3	2.3	8.9	6.9	2.3
September	19.0	7.1	11.6	16.1	6.4	2.6	3.6	8.4	9.5	3.4
October	16.1	8.2	23.9	20.0	9.0	4.1	6.7	14.8	10.2	2.2
November	10.9	10.0	18.2	20.7	9.0	5.0	8.9	15.7	16.4	9.4
December	4.8	10.4	15.1	19.4	10.4	8.7	8.5	13.2	19.3	6.6
Total	109.3	92.9	144.7	177.6	94.0	70.9	74.7	125.9	127.2	75.8

heavy storm a large proportion of the rain is precipitated during a relatively short space of time. Haines has pointed out that each soil has a certain limit for the rate at which it can absorb rain by percolation; and it is the quantity which falls in excess of this that accumulates and runs over the soil surface and constitutes the major factor in erosion.

In Burma the rainy season is from May to October during the south-west monsoon and practically the whole of the rain is precipitated during this period. In Malaysia no such seasonal differences can be marked although in the northern part of the Malay Peninsula there is a very slight

tendency towards seasonal changes: in the Langkawi Islands and off the coast of Kedah the force of the south-west monsoon is felt occasionally. The north-east monsoon, which rages in the China Sea between November and March, is not without effect on the east coast of Malaya and for a month or two during the year Pulau Tioman and Pulau Aor are cut off from the mainland by rough seas. Violent squalls of short duration, known as "Sumatras," occur quite frequently in the Straits of Malacca.

In equatorial regions, particularly those with the type of climate which occurs in Malaysia, variations in barometric pressure are regular besides being negligibly small: consequently altitudes can be determined by means of an aneroid barometer.

THE WEATHERING OF ROCKS AND SOIL FORMATION

The soil, comprising as it does an admixture of mineral fragments derived from the underlying rocks and particles of organic matter resulting from the decomposition of dead vegetation, is a highly complex material showing considerable variation in composition from one locality to another. At first sight it would be anticipated that the soil would be closely related to the rock formation underlying it and that a classificatory system would be based on such a relationship. It is now generally recognized that soils are related primarily to the climatic conditions under which they are formed, and only indirectly to the parent mineral material. In short, soil is the product of the action of climate upon rocks.⁸

The weathering of rocks, resulting in the production of minute mineral particles, is an essential process in soil formation: in temperate regions this disintegration is essentially physical, being effected by such factors as a wide range of temperature change (resulting in alternate contraction and expansion of the rocks), the action of frost and glaciers and wind erosion but, undoubtedly, carbon dioxide dissolved in rain water plays some small part. In the humid tropics the weathering of rocks is almost

exclusively a chemical process; in such regions the temperature is high and, in consequence, the solvent action of rain water is much increased. Although the temperature falls as the hills are ascended, throughout almost the whole of Malaysia climatic conditions are such that, even at the highest altitudes, weathering is effected by chemical and not by physical means.

LATERITE

The fundamental importance of the relation between precipitation and evaporation in the weathering of rocks was first recognized by Hilgard⁹ but the subject has been examined in detail by Mohr as far as Java and Sumatra are concerned. Three cases arise which can be classed as follows:—

(a) *Rainfall exceeds evaporation throughout the year.*
("Humid" regions.)

Much of the water escapes by a downward movement through the soil and this percolating water dissolves soil gases, any soluble organic material and, to a lesser extent for a reason which will appear later, mineral salts. There is thus a continual leaching into the subsoil of mineral salts and any soluble organic matter, much of which finds its way eventually into rivers and then into the sea, and the whole process is one of soil impoverishment.

(b) *Evaporation exceeds rainfall throughout the year.* ("Arid" regions.)

In this case the rain falling on the soil during a shower does not percolate to any depth but soon passes upwards and is lost by evaporation. The ascending solution contains salts derived from the subsoil and underlying rock and this results in a concentration of soluble mineral material at the surface of the soil. It is interesting to note that all the great civilisations whose development was agricultural rather than intellectual have grown up in such arid regions as, for example, Peru, Mesopotamia, Egypt and Assyria.

(c) *Alternation of wet and dry seasons.*

These conditions obtain in temperate regions, such as Europe and North America, but, compared with the tropical zone, the rainfall is slight and the temperature low so that no appreciable upward and downward movements of soil material are to be expected.

It is evident that Malaysia falls into the class (a) where rainfall exceeds evaporation and there is a continual downward movement of water resulting in soil impoverishment. Given an infinite expanse of primary forest, the method of agriculture employed by certain of the aboriginal races of Malaysia (e.g. the Sakai "ladang" method) is probably the correct one under the circumstances. A small area of forest is cleared and a few crops are grown but, as soon as the inevitable impoverishment of the soil sets in, the ladang is abandoned and the cultivators seek pastures new and leave time to deal with the forsaken clearings. Once a limit is set on the area of land available for cultivation, however, such methods cannot be employed to any appreciable extent.

In the humid tropics, where there is a constant downward movement of water through the soil as a result of the excess of rainfall over evaporation, the final product of weathering is remarkably similar throughout the world and is the yellowish- to brownish-red material underlying the top-soil, and so frequently seen exposed at the roadside and elsewhere. The ultimate product of such weathering is usually referred to as *laterite*, but this term was first used by Buchanan¹⁰ in 1807 to connote an indurated clay, full of cavities and pores and containing a very large quantity of iron in the form of red and yellow ochres, overlying the granite in Malabar; when first quarried this material could be cut into bricks and hardened by exposure. This quarried laterite is still used to a small extent in building and was employed by the Portuguese for the sixteenth-century church of St. Paul's at Malacca. The term is now generally applied to the weathered products formed *in situ*, rich in alumina and iron oxide, designated *lixivium* by Mohr, and this misuse of the word is so usual that there seems little



TERRACING AS A PROTECTION AGAINST LANDSLIDES ON A LATERITE
SLOPE ON THE ROADSIDE.

purpose in attempting to restrict the term to its original meaning. The definition of laterite has been subject to much discussion and in this book the term is employed in its popular sense unless the contrary is stated.¹¹

According to Mohr, the continuous action of warm rain water on rocks results in the removal of practically all materials except iron and aluminium oxides, though where an impervious substance such as quartz occurs it persists unchanged with the alumina and iron oxide in the laterite.

The question of the formation of humus in the humid tropics is discussed on page 99, but it may be stated here that, under the usual conditions of temperature and humidity prevailing at low elevations in Malaysian forests, humus destruction takes place almost as fast as its formation so that, in general, practically no accumulation of organic matter takes place. Silica and kaolin are more soluble in water in the absence of carbon dioxide and organic matter than in the presence of these substances but with the oxides of iron and aluminium the reverse is the case. Thus, continual leaching by water containing little or no dissolved organic matter results in the Malaysian soils being impoverished as far as silica and kaolin are concerned, while there is a gradual accumulation of iron oxide and alumina. Thus it comes about that laterite is so characteristic a feature of the humid tropics throughout the world, and it is on laterite slopes that landslides are so prevalent. The depth to which this type of weathering occurs is often remarkable and it is not extraordinary for road-making operations to disclose soft weathered mineral material at depths from 50 to 100 feet under primary forest. Completely weathered laterite is very infertile and of little use to the agriculturist.

Iron and aluminium oxides are comparatively soluble in water containing organic matter, and it will often be observed that water in ditches in plantations on peaty soils which have been drained is deep reddish-brown, the colour being due largely to dissolved ferric material.

Mohr states that in some parts of Java, where there is a tendency towards the alternation of wet and dry seasons, in the presence of alkaline salts the climatic conditions

result in the formation of a black and not a red soil. Under such circumstances leaching occurs during the wet season and during the dry months the salts in solution are brought to the surface again where they react with the organic matter present to produce a black soil. With such soils the percolating water frequently contains dissolved organic matter and, in consequence, iron oxide is taken into solution and may be deposited as a solid concretion some depth below the surface. This secondary rock formation in the soil, however, occurs the world over but is usually very local: the deposition of material rich in silicic acid is a feature of arid regions while the formation of concretions rich in ferric hydroxide, such as "hard pan" and ortstein, is a world-wide phenomenon.

The reverse of *laterization* is *podsolization* which takes place in the lowlands in temperate regions and, to a limited extent, in the high mountain zone of Malaysia.¹² In this process water laden with organic matter percolates through the soil resulting in a relative increase in silica in the upper horizon and a diminution in the content of iron oxide and alumina.

CLASSIFICATION OF SOILS

Although all mature soils formed under the same conditions of temperature and humidity approximate to the same composition in whatever part of the world they may have originated, it is evident that recently formed soils are much more closely related to the parent rocks from which they were derived. It has been stated that the composition of the soil is primarily a function of the climate but, nevertheless, in comparatively recent formations such as occur in Malaysia the relation between the soil and the parent rock may be sufficiently close to admit of a soil classification on this basis. An attempt at such a classification of the soils of the Malay Peninsula has been made by Belgrave and Dennett.¹³ A certain amount of soil cartography has been carried out in Sumatra and Java.¹⁴

According to Arrhenius,¹⁵ continual leaching of soil in the humid tropics results in an increase in the degree of acidity,

so that the pH value¹⁶ of a soil gives some indication of its age and degree of impoverishment. Martin found that low pH values are associated with high rainfall: in north Sudan, where the rainfall is low (about 3 inches per annum), the average reaction of the soils is about 9.5 but in Sierra Leone, under a rainfall of 180 inches per annum, the average value is 4.5. Malayan soils range from pH 4.7 to 5.5, while the coastal peat soils are even more acid.¹⁷ Low pH values are associated with low figures for soluble potassium and phosphate.¹⁸

SUMMARY

The Malay Peninsula, Sumatra, Borneo, Java, Palawan and the adjacent small islands, constituting the faunistic sub-region of Malaysia, were once united to form a continent (Sundaland) and still exhibit remarkable uniformity in geological formation, flora and fauna. As in other parts of the equatorial belt, the climate of Malaysia is characterized by a uniformly high temperature (80° F.) and heavy rainfall (100 inches per annum) and the atmosphere is very humid: the temperature falls as the hills are ascended.

Under these climatic conditions, weathering of the rocks is largely a chemical process, resulting in the formation of lateritic soils, characterized by low silica and high sesquioxide ($Al_2O_3 + Fe_2O_3$) content, and it is the presence of iron oxide which gives these soils a red or reddish-yellow colour.

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Laterite .. $\text{SiO}_2/\text{Al}_2\text{O}_3$ ratio 1.33 and under.
 Lateritic .. $\text{SiO}_2/\text{Al}_2\text{O}_3$ ratio between 1.33 and 2.0.
 Non-lateritic $\text{SiO}_2/\text{Al}_2\text{O}_3$ ratio 2.0 and above.

Some investigators employ the $\text{SiO}_2/(\text{Al}_2\text{O}_3 + \text{Fe}_2\text{O}_3)$ ratio rather than the silica/alumina ratio, but Martin and Doyne do not regard iron as an essential constituent of laterite soils. Recent work by F. Hardy (*J. Agric. Sci.*, 1931, **21**, 150-166) indicates that it is the silica/free alumina ratio which is important in this connection.

M. S. Anderson and S. Mattson (*U.S. Dept. Agric. Bull.*, 1452, p. 46 [1926]) have shown that a linear relationship exists between the ammonium ions absorbed by different clays and their $\text{SiO}_2/(\text{Al}_2\text{O}_3 + \text{Fe}_2\text{O}_3)$ ratios. In laterite and lateritic soils, where the silica/sesquioxide ratio is low, the absorption of ammonium ions is low so that it would be anticipated that free ammonia would be present in measurable quantity in the soils of the equatorial belt. R. G. H. Wilshaw (*Malayan Agric. J.*, 1934, **22**, 4-24) has shown that such free ammonia does in fact exist in Malayan soils and can be removed by leaching. Clay becomes unstable in presence of high rainfall and, usually, is not present in large amounts in soils of the humid tropical regions.

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EPIPHYTES ON *ENTEROLOBIUM SAMAN*.

II. THE PLANT LIFE OF MALAYSIA

BEFORE the advent of civilized man, practically the whole of Malaysia was covered with dense, primeval forest, except for estuarine areas on some of the coasts which supported mangrove associations. The Malaysian forests are denser than those on the Asiatic mainland and differ in certain other respects: they are exceedingly damp and are richer in species of plants and animals than in individuals. Naturalists in temperate climates are prone to visualize the jungle of the humid tropics as sunlit forest in which a boundless variety of brightly-coloured birds and insects flourishes amid a luxuriant plant growth, but very rarely is such a picture realized. The tropic jungle is often sombre in the extreme, the canopy being so dense in some places that the sun never penetrates and consequently the atmosphere is very moist. In the forest itself butterflies are not much in evidence; once the sun is up birds are rarely seen or heard and the feeling experienced by the solitary wanderer of being watched by invisible and, perhaps, hostile eyes tends somewhat to deepen the gloom and to fill him with vague apprehensions. Nevertheless the jungle is not usually silent except during the few moments that precede the breaking of a tropical storm. Sometimes the chatter of monkeys adds a lively note and they can be heard crashing through the tree-tops; squirrels are seen quite frequently and on almost any bright day the curiously monotonous and ventriloquial call of the cicada rings shrilly through the woods. Although large mammals are rarely seen, it is soon appreciated that they are not necessarily very distant and it behoves a solitary human to walk warily. To convey any adequate picture of the Malaysian forest is difficult but, for those who can appreciate the immensity of the natural forces at work and be aware of the great antiquity of many of the plant and animal associations, truly the forest is enchanted.

In primary forest, trees and large shrubs predominate and herbaceous plants are not common. Many of the tree-trunks are of enormous dimensions and are supported by large buttresses at the base, and some of the tallest trees pertaining to the Dipterocarpaceae are remarkable for the absence of branching. From the crowns of many giants of the forest trail creeping lianas and most of the larger trees bear numbers of such epiphytes as orchids and ferns on their boughs. Usually there are relatively few trees with trunks of small diameter, but fair-sized shrubs flourish where space permits and it is often difficult to make a passage through the forest on account of the many palms, such as rotan (*Calamus*), possessing hooked spines which impede progress. Of the spiny palms, the large bertam (*Eugeissonia tristis*) is remarkable in that it is practically stemless and grows in large clumps. Flowers are not encountered frequently, the reason being not that they are necessarily rarer than in temperate regions but that there is no definite flowering season and most plants blossom at rather irregular periods: moreover, the majority of the flowers are of small size and of a greenish hue and consequently are overlooked among so much foliage. On the other hand, trees are found occasionally which display a mass of brightly coloured flowers, constituting a powerful attraction to bees and to large and richly ornamented butterflies. In some localities, both on the plains and in the mountains, large patches of bamboo occur and in such areas these plants predominate very largely to the exclusion of other forms of vegetation.

To the ordinary observer, with a limited knowledge of botany, there may appear to be little difference in the density or the species of plants at elevations between sea level and 5000 feet; but many plant species are confined to the plains while others occur only on the hills. Large tree ferns (*Dicksonia*, *Cyathea* and *Alsophila* species) are a feature of the forested hills at elevations of 2000 feet and above and the remarkable pitcher plants (*Nepenthes*) are rarely found in any profusion below 4000 feet. In some localities, however, a marked change in the flora can



RHIZOPHORA TREE IN MANGROVE FOREST. NOTE THE PNEUMATOPHORES
AND THE VIVIPAROUS FRUITS IN THE MUD IN THE FOREGROUND.

be detected when certain altitudes are reached. In parts of Pahang, at elevations of over 5000 feet the forest becomes less dense, the more massive trees disappear and certain species of flowering plants such as the Himalayan violet (*Viola serpens*),¹ *Sanicula europea* (a member of the wild parsley family), *Ophiopogon intermedius* and golden balsam (*Impatiens oncidoides*), which are rarely seen below 4000 feet, become evident: in fact, at this height, the forest begins to take on some of the character of European woodland. These Himalayan plant species occur only in a restricted area in the Malay Peninsula and the first three named are found at high altitudes in Sumatra and Java; recently *V. serpens* and *S. europea* have been reported from Mount Tibang in the centre of Borneo.

In primary jungle the forest floor is covered with a pall of damp dead leaves and twigs and it is surprising how noiselessly large animals and the aboriginal tribes move about.

In Malaysia, the composition of the vegetation comprising primary forest bears little relation to the underlying geological formation but in some localities, such as the Langkawi Islands, the stunted growth of the forest on limestone compared with granite is striking. In the Malaysian forests the diurnal variations in temperature are but slight: the temperature of the soil is practically constant at 75° F. (24° C.), the daily variation even at the surface being less than 1°.

MANGROVE FORESTS

The mangrove forests fringing the coasts are of particular interest, although the flora is confined almost entirely to the Rhizophoraceae, Verbenaceae, Lythraceae and Meliaceae.² Species in the first-named order predominate, their stilt-like roots and curious clusters of respiratory root suckers (*pneumatophores*) projecting from the mud constituting very characteristic features of the mangrove forests. The fruits of the Rhizophoraceae and a few species pertaining to other orders are viviparous, germinating while still united to the parent and then falling vertically into the mud beneath

and taking root. Viviparity in plants is confined exclusively to species occurring in tropical mangrove swamps.

The nipah palm (*Nipa fruticans*) is an important species found in mangrove plant associations, but, under natural conditions, pure stands do not occur to an appreciable extent in the Malay Peninsula as they do in North Borneo. The nipah palm is used as a source of alcohol in the Philippines and an attempt has been made to cultivate it for this purpose in Malaya, where its primary use was as a thatching material.

The trees in mangrove forests do not attain the heights found in primeval jungle but the canopy is often sufficient to give considerable shade to the forest floor. There is a certain amount of local variation in the undergrowth: leguminous plants are scarce, in fact, Watson lists two species only. Mangrove forests constitute a source for the supply of firewood, the bulk of "bakau" firewood sold in Malaya being obtained from *Rhizophora conjugata*, the dominant species in the usual plant association found in Malaysian mangrove areas.

THE EFFECT OF CLEARING FOREST

It is a matter of everyday experience that, even in the humid equatorial regions, forests do not arise shortly after cultivated land is abandoned but they constitute the climax in a series of plant associations which appear in turn when nature is given a free hand. The whole series of changes which precedes the establishment of normal forest³ is very complex and considerable modifications may result from but slight changes in local conditions. In Western Europe, where land is rarely abandoned and left undisturbed for decades, the problem of secondary growth is of little consequence, but in the humid tropics, particularly at the present time, when large areas of cultivated land are being neglected, this question is of considerable importance.

The ultimate consequences of forest clearing in Malaysia are of much interest and not without economic importance. Most of the clearing that has taken place in the Malay Peninsula during the last decade or so has been for the purpose of

opening up land for the growth of rubber, and the *modus operandi* has always been the same. Timber of economic value is removed and the remaining jungle growth is entirely felled, and burned as far as possible. The soil is thus exposed to the sun and bereft of all shade until such time as rubber seedlings are planted. The entire history of a rubber estate was, and in many cases still is, a prodigal squandering of natural resources; so that when an old plantation is finally abandoned the soil is so much impoverished that many years must elapse before the plant association can bear any resemblance to the primeval forest which was ousted.

Before considering in detail the reversion of a completely cleared area to primary jungle it is instructive to examine the results of partial clearing of forest, such as frequently takes place through the agency of Chinese wood-cutters in the Malay Peninsula. These wood-cutters are permitted to fell certain species of trees not exceeding a stated diameter and to do this effectively the smaller shrubs and undergrowth are removed, so that finally almost only the large trees are left, though the floor of the forest may still be shaded adequately. With such partial clearing, the nature of the secondary growth is to a large extent dependent on the degree of shade remaining, and if there are sufficient numbers of large trees to ensure the forest floor being still heavily shaded, ginger plants (Zingiberaceae) appear and soon become the dominant feature of the flora. As time goes on, other plants obtain a footing and the Zingiberaceae gradually drop out, but for a long time such forests are characterized by a rather heavy surface growth, which disappears only when new trees and shrubs have attained reasonable dimensions.

When clearing has been more drastic and the forest floor is left partially exposed to sunlight, the secondary growth follows a different course and, in these circumstances, the ground is soon densely covered with low-growing grasses, such as *Andropogon aciculatus*, which act as an effective check to other competitors. In the course of time low-growing shrubs such as Straits rhododendron (*Melastoma polyanthum*) appear, and once they obtain a footing and the

forest floor is effectively shaded, the grass gradually disappears and the way lies open for larger shrubs and trees to become established.

Shade is a factor of vital importance in determining the subsequent history of cleared jungle areas. In the first instance outlined above where ginger plants have predominated in secondary growth, it is a matter of a few years only before the cleared area begins to resemble a forest again; and it seems probable that the vegetation following the Zingiberaceae largely comprises trees and shrubs which are definitely indigenous to the primeval forest. In cases where grass has become established, however, the subsequent cycle of change is very different and, for many years, the plants predominating are those which find no place in primary jungle. Incidentally, at the jungle edge there is usually a very profuse and tangled mass of low-growing vegetation, and the forest floor is so thickly covered that penetration is difficult and often impossible without the aid of a *parang*. Visitors to these tropics who have never entered the jungle are apt therefore to receive a somewhat false impression of its density.

LALANG

When the original jungle has been felled and cleared in the customary manner and the soil is left exposed to the sun, in a remarkably short space of time the whole of the abandoned area is covered with a dense growth of a tough, leathery spear-grass known as lalang (*Imperata arundinacea*). This is the "alang-alang" of the Malays and once established its eradication is a matter of considerable difficulty: it grows rapidly, attaining a height of several feet, and for a year or two it flourishes to the total exclusion of all other plants. It appears to be remarkably immune from attack by insects and fungi and is reported to occur in all the humid tropical regions of the world: it is doubtful if it is indigenous to Malaysia. There is a generally accepted belief among the planting community in Malaya that lalang grows only on "good" soil; but it may well be that the reverse is the case and that it can do well on soil which is



LALANG GRASS IN A COCONUT PLANTATION.

unable to satisfy so readily the more exacting requirements of other forms of vegetation. Actually it would appear that the only condition necessary for the vigorous growth of lalang on the plains of Malaysia is a soil exposed to the sun.

Once lalang has become established on a rubber plantation it can be removed only by digging out each separate plant by its root: it has been stated that, when lalang has been cut down or burnt, it subsequently flowers freely and thereafter spreads in an alarming manner. It is generally accepted that lalang has a deleterious effect on the growth of rubber trees: there is no evidence to show that this plant is responsible for the elaboration of toxic substances but, according to Vageler⁴ it vigorously promotes ortstein formation (see page 22) in acid soils. The risk of fire as a result of the presence of lalang is a real one as it burns furiously even when in vigorous growth, giving off great heat, and this fact, coupled with the difficulty of keeping the weed under control, demands steps to discourage its increase as far as possible on rubber estates. Lalang has a very dense and matted root system which is probably a deterrent to sun-loving plants which might otherwise compete with this pest. Other plants appear in lalang areas only after a considerable lapse of time: *Lantana aculeata* and Straits rhododendron (*Melastoma polyanthum*) are among the first and most conspicuous of these, although the former is not native to Malaysia, having been introduced from Jamaica by Lady Raffles, according to some authorities. Gradually, larger shrubs appear and as the ground shade is increased the lalang growth is reduced; but this plant maintains its stranglehold on the soil for some years before it ceases to be the dominant species of the flora.

In the Malay Peninsula lalang does not appear to flourish on the hills much above 3000 feet, but vast tracts of the Battak plateau in Sumatra at elevations of about 4000 feet are covered with it. When primary jungle is removed on the Malayan hills, the secondary growth usually consists largely of bracken (*Gleichenia linearis*) but a dense and low-growing grass appears in some situations.

Imperata arundinacea and *Lantana aculeata* are two of the commonest weeds in Malaysia and it is certainly curious how the entry of a plant or animal into a new faunistic region is so often fraught with disastrous consequences. A few of the many similar cases can be instanced: the European rabbit which has become a pest in Australia; a Japanese cockchafer beetle which does untold damage annually to certain crops in North America and the American musk rat

TABLE IV
COMMON MALAYSIAN PLANTS WITH COUNTRY OF ORIGIN

Name.	Family.	Country of origin.
<i>Allamanda cathartica</i>	Apocynaceae	Tropical America
<i>Andropogon aciculatus</i> Love grass	Gramineae	Tropical Asia to Australia
<i>Antigonon leptopus</i> Honolulu creeper	Polygonaceae	Tropical America
<i>Asclepias curassavica</i>	Asclepiadeae	West Indies
<i>Bougainvillea glabra</i>	Nyctagineae	Tropical America
<i>Caesalpinia pulcherrima</i> Peacock flower	Leguminosae	West Indies
<i>Casuarina equisetifolia</i>	Casuarineae	North Australia
<i>Crotalaria anagyroides</i>	Leguminosae	Tropical America
<i>Eichhornia crassipes</i> Water hyacinth	Pontederiaceae	South America
<i>Enterolobium saman</i> Rain tree	Leguminosae	Tropical America
<i>Fagraea fragrans</i>	Loganiaceae	Malaysia
<i>Hibiscus rosa-sinensis</i> Garden hibiscus	Malvaceae	Probably Malaysia
<i>Ipomoea learii</i> Morning glory	Convolvulaceae	Tropical America
<i>Lantana aculeata</i>	Verbenaceae	Tropical America
<i>Melastoma polyanthum</i> Straits rhododendron	Melastomaceae	Probably Malaysia
<i>Mimosa pudica</i> Sensitive plant	Leguminosae	Tropical America
<i>Plumeria acutifolia</i> Temple flower	Apocynaceae	Tropical America
<i>Ravenala madagascariensis</i> Traveller's palm	Scitamineae	Madagascar

which is becoming a menace in western Europe. The giant snail (*Achatina fullica*) was introduced into India from Africa over seventy years ago and in about 1900 the species became established in Ceylon: before 1922 it was found in the Malay Peninsula and, during the last few years, it has spread

rapidly there to become an important pest in gardens. The giant snail reached Sarawak in 1928 and was already a pest by 1931: during a fortnight in October, 1931, approximately half a million snails and twenty million eggs were destroyed.⁵ *Mimosa pudica*, the sensitive plant, which is so abundant in grassy, sunlit areas in Malaysia, was introduced from America.

It is often averred that the reason for introduced species of plants and animals becoming so prolific in a new faunistic region is to be found in the absence of their natural checks. It is evident that such an explanation accounts for very few cases: the subject is one of economic importance and another explanation is suggested on page 68.

It is not generally realized what a large proportion of the conspicuous plants growing in gardens and waste places in Malaysia have been introduced from other parts of the world: a list of some of the commoner plants with the country of origin is given in Table IV.

SUMMARY

The climax of the vegetation in Malaysia is the tropical rain forest, characterized by a number of storeys, of which the topmost provides a dense canopy. The tallest forest trees, which pertain to the family Dipterocarpaceae, are notable for the complete absence of branching until the crown is reached. An abundance of epiphytes and trailing lianas contribute to the riotous growth of the jungle. A feature of these forests is the paucity of individuals representing the numerous species.

When primary forest is felled and cleared, in the absence of cultivation, there first appears the pernicious lalang grass (*Imperata arundinacea*), and a year or two elapses before low-growing shrubs and leguminous plants gain a footing. Eventually the lalang dies out and trees come in, but many decades must pass before such secondary associations bear any resemblance to primeval forest.

Apart from cultivated crops, the only other vegetation type which covers any area in Malaya is the mangrove association, found in muddy estuaries and elsewhere on

sheltered coasts. In this community, the Rhizophoraceae predominate. Many of the trees in mangrove swamps are of particular interest on account of their stilt-like roots, pneumatophores projecting above the mud and viviparous seeds.

REFERENCES

1. According to H. N. Ridley (*The Flora of the Malay Peninsula*, 1922-1925, 5 vols, Ashford, Kent) this species formerly occurred on Penang Hill at 3000 feet, but is now extinct.
2. J. G. Watson, "Mangrove Forests of the Malay Peninsula," *Malayan Forest Records*, 1928, No. 6.
3. Normal forest is that in which the distribution of the age classes is in the proportion required to produce the same yield perpetually: A. H. M. Barrington, *Burma Forest Bull.*, 1931, No. 25.
4. P. Vageler, *An Introduction to Tropical Soils*, translated by H. Greene (London), 1933.
5. V. H. C. Jarrett, *Hongkong Naturalist*, 1931, 2, 262-264.

III. THE SOIL FAUNA

ON old coconut and rubber plantations in Malaysia, where the bulk of the original soil organic matter has long since disappeared, dead rubber or coconut leaves offer no great attractions to insects or other small invertebrates, and such areas are usually remarkable for the paucity of the soil fauna. A different state of affairs exists in the soil under forest for, although at first sight it does not appear to be teeming with life, closer inspection shows that a considerable soil population exists. It appears that the soil macro-fauna presents an analogous case to the tropical forest fauna in that a large number of species are represented by comparatively small numbers of individuals.¹ Many animals pass the whole of their lives in the soil and many more spend some part of it below ground. Most of the larger soil invertebrates are found under the roots of trees and shrubs and in the neighbourhood of buried timber.

Invertebrates affect the soil in which they live in several ways:—

- (a) their passage through the soil results in improved aeration and, possibly, in better distribution of the plant nutrients present;
- (b) the deposition of their excreta indicates a quick return to the soil of organic and mineral matter which would otherwise be retained in growing vegetation;
- (c) in cultivated areas they may damage certain crops.

In considering the soil macro-fauna, the subject will be dealt with under three heads:

- (a) primary forest;
- (b) cultivated areas;
- (c) mangrove swamps.

While (b) is the most important from the agricultural standpoint, the fauna of the primeval forest is much richer and will be considered in greater detail.

PRIMARY FOREST

Apart from a very few species of mammals there are no vertebrates normally resident in the forest soil in sufficient numbers to play a rôle of any importance. In the Arthropoda, some orders of insects, notably Lepidoptera (butterflies and moths), Hymenoptera (ants, bees and wasps), Coleoptera (beetles), and Diptera (two-winged flies) are represented by many species passing the early stages under ground, but several species of ants and beetles spend all their lives on or just below the surface. From the standpoint of the soil biologist, the most important insects are the Isoptera (termites), which creatures, to a certain extent, take the place occupied by earthworms in colder climates.

Termites.

Termites, popularly known as "white ants," live in communities much in the same manner as do certain species of bees and ants. The nest is known as the *termitarium* and contains numbers of individuals belonging to different castes, the members of which serve the rest of the community in the manner to which they are each peculiarly fitted. The winged forms, which are only too familiar at the lights of bungalows during certain periods of the year, comprise males and females which are sexed in the usual manner. After the nuptial flight a male and female, or rather "king" and "queen," establish a colony and, from the ova produced by the queen, individuals are born in which the sex organs are aborted. The majority of these sexless termites are "workers" whose functions comprise constructing and attending to the *termitarium*, feeding the royal pair and the immature forms (*nymphs*) and, in the case of certain species, cultivating the fungus gardens. The soft-bodied workers are quite blind, and have to rely entirely for their protection on the "soldiers." The latter have prominent, hard heads and are equipped with powerful

mandibles: their primary function is to keep off invaders while the workers repair any breaches in the walls of the termitarium.

Once a colony is established the queen produces ova at a prodigious rate; the abdominal segments of her body become greatly distended and often she attains an enormous size. For the rest of her life she remains imprisoned in the royal cell with the king, whose sole function is to fertilize the queen. At some periods of the year the sexed winged forms are produced in vast numbers and, when certain climatic conditions obtain, they leave the termitarium together at dusk and the comparatively small proportion that escape destruction establish new termitaria.

Some one hundred and forty species of termites are already known from Malaysia and some of them are characterized by the very distinctive nature of the termitaria constructed.² Many species appear to reside in decaying timber, others nest deep underground and a few species are mound builders. Some of the mounds constructed attain a height of 5 or 6 feet, but the mound builder most frequently encountered in Malaysia is *Macrotermes gilvus* of which the mound is low and, when covered by vegetation, is not conspicuous.

The sexless castes of termites abhor the daylight and when it is necessary for them to travel from one spot to another a mud tunnel is constructed under cover of darkness. The termites resident in the soil play an important rôle in effecting the decomposition of fallen timber. Such material has a high carbon/nitrogen ratio and its decomposition by bacterial or fungal activity would not only be slow but would entail the temporary loss of a certain proportion of the soil nitrogen in the cells of the micro-organisms. Although the chemical effects of termites in the soil have not been investigated in any detail, it seems tolerably certain that termites are the most active agents in bringing about the decomposition of timber in the forest. It has been shown that, in the course of the digestion of wood by the Australian mound builder *Eutermes exitiosus*, a considerable decomposition of the cellulose occurs but

the lignin remains almost unchanged.³ The ceaseless movements of termites through the soil hasten the decomposition of decaying vegetation effected by microbiological activity, by increasing the aeration.

The small termites which infest the timber of dwelling houses appertain to the genus *Cryptotermes*.

Other Insects

Ants are important for much the same reasons as are termites, but their good works must be assessed at a much lower value. Apart from their movements which assist the aeration of decaying vegetation, they serve a very useful purpose in removing carrion and all dead animal matter. The speed with which these creatures work has to be seen to be believed and, at any time, immediately an insect falls helpless on the forest floor it is removed by ants. It is very unusual indeed to find any dead creature or excrement in the forest and the rapid return of the nitrogen in such material to the soil is attributable to the activities of the ants. In short, ants are responsible for the speedy decomposition of animal organic matter while termites effect the breakdown of some of the more refractory vegetable materials. Ants do not confine their attentions exclusively to dead animal bodies, many species preying on other insects: in fact, the pugnacious tree ant or "kerengga" (*Oecophylla smaragdina*) was employed to clear cultivated crops of insect pests until it was discovered that the remedy was as bad as the disease.

The other insects occurring in the soil are probably of relatively small importance. Larvae of wood-boring beetles possibly play some small part in the cycle whereby timber is transformed into a form in which it can be utilized as plant food. The grubs of many species of beetles, however, are to be found below ground and their presence is undesirable only when they cause damage to growing vegetation by feeding on the roots: the dung beetles (Coprinae) enrich the soil by burying excreta and the sexton beetles (Silphidae) help to bring about the rapid disintegration of animal

carcasses. Cockroaches (Blattidae) and earwigs (Forficulidae) are not uncommon among the debris on the soil surface: to many lepidopterous larvae and pupae the soil serves as a refuge.

Earthworms

Although earthworms (Oligochaeta) occur commonly in Burma, they are by no means abundant in Malaysia and they can play no essential part in the equatorial tropics in increasing the fertility of the soil in which they live. The commonest Malayan species, *Pontoscolex corethrurus*, is generally distributed and in habits resembles the common European species of *Lumbricus*. Occasionally these animals may be turned up in some numbers but usually only odd examples are seen: they are much more abundant in the Langkawi Islands than on the mainland of the Malay Peninsula, but it has already been pointed out that north Kedah (including the Langkawi Islands) shows affinities with south Burma as regards both flora and fauna. Incidentally, *Pontoscolex corethrurus* is common in south Burma. Dammerman reported the Enchytraeid *Fridericia bulbosa* as a common species in Sumatra and Java, occurring from the seashore to the top of Mount Gedeh (9800 feet). A few Malaysian species of earthworms attain enormous dimensions; the Sumatran species *Moniligaster houteni* often exceeds a yard in length.

In temperate regions earthworms are able to raise the level of the soil by throwing up wormcasts¹: they are sensitive to the reaction of the soil and do best when the pH is not more acid than 6.0.

The minute, unsegmented roundworms or eelworms (Nematoda) are abundant in the surface layer of tropical soils, but they have attracted little attention in these regions. Many of the species are free-living saprophytes, utilizing dead vegetation and playing a part in the transformation of soil organic matter and in improving the soil aeration. Some species consume micro-organisms and others, in

cultivated areas, often effect considerable damage to cultivated crops.

Woodlice (Oniscoida) are the commonest representatives of the Crustacea in the soil surface debris and, of the Myriapoda, centipedes (Chilopoda) and millipedes (Diplopoda) are fairly common. Ground spiders (Arachnida) are to be found almost everywhere and the same may be said of some of the smaller species of snails (Mollusca).¹

The character and concentration of the forest soil fauna varies with altitude (see Table V); in general, species which are characteristic of the tropics tend to disappear as the

TABLE V
THE DISTRIBUTION OF THE SOIL FAUNA WITH ALTITUDE IN JAVA

Height in feet on Mount Gedeh, Java.	Average number of species found in debris on 1 square metre of soil surface.
4500-5500	53
6500-8000	30
9800	11

K. W. Dammerman, *Treubia*, 1925, 6, 107-139.

mountains are ascended. Termites are absent above 5000 feet, ants disappear at about 6500 feet and cockroaches are not found above 8000 feet. The woodlice decrease in numbers as the mountains are ascended, but sandhoppers (Orchestia) are most numerous between 4500 and 8000 feet. Mites are not found above 8000 feet but centipedes, millipedes, ground snails and ground spiders occur at the summit of Mount Gedeh (9800 feet).¹

CULTIVATED AREAS

On the older rubber estates, many of which have been "clean-weeded" for a number of years, the soils have a hard surface layer and are deficient in humic material. The rubber leaves decompose but slowly, giving only a shallow surface layer so that, generally, rubber plantations have little to offer to insects. Nevertheless, any soil insects which stray to rubber estates have a clear field

and are not liable to suffer heavily from attack by natural enemies.

Ants are common on rubber estates, as they are almost everywhere in the humid tropics, and nest in old timber or under the soil surface; but their presence is of little account for most of them travel above ground were possible. The presence of buried timber on estates, coupled with the old "clean-weeding" methods, makes attractive conditions for certain species of termites, some of which can become a veritable scourge, having been known as a pest to rubber trees from the earliest planting days.

Two species of termites are of importance on rubber estates: one of these is the common and widely distributed mound builder, *Macrotermes gilvus*, and there appear to be no reliable records of its having perpetrated any damage to rubber. This species favours rather low-lying land on or in the vicinity of rubber estates, and the low mounds are hardly noticeable where there is a good cover. The nest is honeycombed with tunnels and contains a number of fungoid, sponge-like masses, the "fungus gardens," which are constructed by the workers from partially digested wood and leaves and used as food for the young. In the queen the abdomen is often greatly distended and may attain a length of two and a half inches. Much money has been wasted in Malaya in attempts to eradicate *M. gilvus* from rubber plantations under the mistaken notion that this insect is responsible for the damage caused by the following species. In any case the method of paying a bonus to coolies for each queen found is futile, as new queens can easily be reared!

Coptotermes curvignathus is a serious pest of rubber both in Sumatra and in the Malay Peninsula.^{5,6} It has often been recorded in Malaya as causing damage to living rubber trees, but there appears to be a general impression that the species confines its attention to trees which are diseased: it can now be stated that there is no justification for the belief that healthy trees are immune from attack by *C. curvignathus*. The species is common where it occurs and shows a decided preference for damp situations, being

found on low-lying land where moist conditions obtain. It has been found attacking young rubber showing no signs of disease and, if left undisturbed, can inflict fatal injury within three or four weeks. The method of attack is as follows: first, a mud tunnel is constructed on the trunk upwards for a distance of several feet and this tunnel is gradually extended laterally until the whole of the lower portion of the trunk is encased with mud; there can be little doubt that these pests reach the tree by means of a subterranean tunnel. A curious point about the initial stages of the attack is that, during the daytime, the mud-encased trunk contains a great preponderance of soldiers over workers.

Once the mud wall has been completed, the bark is attacked simultaneously at several points, but most strongly near the base of the trunk. The exudation of latex does not appear to deter the invaders and the attack is usually continued until the whole of the lower part of the trunk is denuded of bark. Then the wood is penetrated and numbers of long vertical tunnels are constructed: this is followed by an attack on the root system by which time the tree is injured beyond recovery. When *Hevea* "buddings" are subjected to the ravages of *C. curvignathus*, the upper limit of the mud wall may not extend beyond the point of union of the stock and scion and the termites may concentrate their attack upon the snag. When, as is frequently the case, there is a good growth of cover it is difficult to detect trees which have been attacked until irreparable damage has been effected. From the writer's observations, *C. curvignathus* can kill three-year old trees within a month and, moreover, if treatment is not applied within a fortnight of the first appearance of the termites it is unlikely to be of any avail later on.⁷

It is probable that these assaults are carried out by occupants from a central nest which may be situated some distance underground. The fact that the large numbers of soldiers found in the early stages of an attack subsequently give place to a preponderance of workers indicates that communications are maintained between the termites on

the tree and those in a central termitarium. The queens of *C. curvignathus* have been rarely found and there seems to be no evidence to support the suggestion that this species makes permanent nests in young rubber trees. Once this pest has become established its complete eradication is hardly practicable; formerly, removal of all buried timber was advocated, but there is no reason for supposing that this constitutes an effective means of control. On estates where this costly procedure is practised the timber is collected and burnt, but, during the process of collecting and stacking, the termites are disturbed and leave the timber before any measures are taken to encompass their destruction.

Another species of termite, *Eutermes hirtiventris*, has been found attacking adult rubber trees in Malaya in a manner very similar to that employed by *C. curvignathus*.⁷

During the last few years a few rubber estates in the Malay Peninsula have been visited by the cockchafer beetle, *Psilopholis grandis*, which appeared in numbers on an estate in Java some years ago. The ova are deposited in the soil and the larvae spend the whole of their lives underground, feeding on the roots of growing plants. On estates where these beetles are numerous the march of the grubs underground can be traced by the decay of the vegetation whose roots have been devoured. In the presence of this pest it is impossible to establish a cover. In Malaya two primary parasites of the beetle are known: these are the Scoliid wasps, *Campsomeris javana* and *C. pulchrivestita*. In both cases the female wasps deposit an egg on the well-grown beetle grub and the latter is devoured in a few days after the wasp larva has hatched; a Bombyliid fly, *Hyperalonia tantalus*, is a hyperparasite, its grubs feeding on those of the wasps.⁸

Earthworms are usually of only casual occurrence in estate soils in the Malay Peninsula, but when present they may occur in some numbers over a small area. Earthworms on plantations are generally confined to rather damp situations where the soil is soft: their presence does not necessarily indicate a good soil, for these animals were found in some abundance on an old estate in Malacca where

the soil was almost devoid of organic matter. All the earthworms found on rubber estates in Malaya by the writer are referable to *Pontoscolex corethrurus*.

In secondary growth the soil fauna is a mean between that found in the soil of the primeval forest and that under rubber, but there is no very apparent relationship between the soil surface fauna and that of the vegetation: the surface fauna of bamboo areas is poor, but that under mangrove is intermediate between that of primary and secondary jungle. In most cases, the soil under secondary growth was originally exposed to the sun and, in addition to the loss of soil organic matter, has suffered from a hard-baked surface. Both factors make for a much reduced soil fauna but, with the reappearance of a vegetative cover, soil conditions gradually improve until eventually the soil fauna is comparable with that of the primary forest.

MANGROVE FORESTS

The mangrove swamps have a soil population quite different from that of the primary forest or the cultivated plantation and the animals most in evidence are the Crustacea. The soil is pitted with holes and these are particularly numerous in tidal areas or on the banks of streams.

The larger holes are surprisingly deep and tenanted by various species of crabs which emerge at low tide to seek their prey, consisting of sand-hoppers and smaller creatures. The small and brightly coloured fiddler crabs (*Ocypodidae*), in which one of the claws is enormously enlarged in the male, may often be seen on the mud in hundreds but, at the slightest sign of danger (probably when they feel any vibration through the ground), they dart back into their holes or dig down into the soft wet sand with surprising rapidity.⁹ The chimney prawn (*Thalassima anomala*) also lives in holes in the mangrove areas and throws up soil round the entrance to make a "chimney." The amphibious mud fishes (*Boliophthalmus* and *Periophthalmus*) seem to be equally at home both in the water and out of it. Hermit

crabs (Paguridea) are often abundant some distance from the water.

The subterranean crustacean tunnels occupy a considerable volume but apparently each creature has its own particular burrow and builds a new one only under stress of unusual circumstances, so it is doubtful if the tunnels represent any considerable soil movement.

SUMMARY

In the forests of Malaysia, termites (Isoptera) play an essential part in the extent to which they effect the destruction of timber and other plant debris. Ants (Hymenoptera) are important also in that they are responsible for removal of dead animal bodies and excreta.

Earthworms are usually scarce in the soils of Malaya although, occasionally, *Pontoscolex corethrurus* occurs locally in some abundance.

The soil fauna of the mangrove association differs entirely from that of primary or secondary forest as it consists largely of burrowing species of Crustacea.

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IV. SOIL MICRO-ORGANISMS

FROM the agricultural standpoint, the most important groups of soil micro-organisms are Bacteria, Fungi and Protozoa and the two first-named are much more active than are the Protozoa. In temperate regions, the numbers of bacteria present in the soil greatly exceed those of the fungi and, moreover, their activities are generally of a much more fundamental nature.

Bacteria possess several characteristics which facilitate their division into broad groups. Thus, they may be divided into *autotrophic*, *prototrophic* and *heterotrophic* bacteria: those in the first group derive energy from purely inorganic substances, such as metal salts and carbon dioxide, prototrophic bacteria utilize the elements themselves, while the heterotrophic organisms subsist on complex organic compounds which have been elaborated by other organisms. Autotrophic and prototrophic bacteria are far less numerous than heterotrophic species, but, in many instances, their activities are of vital importance. A few species of prototrophic soil bacteria possess the faculty of fixing atmospheric nitrogen.

A few moulds and yeasts are autotrophic in nature but probably all the soil fungi are heterotrophic and most are *facultative saprophytes*, living on dead organic material, rather than *parasites* which live in or on living organisms. Their importance in temperate climates has not been over-rated but it is evident that they play a much more important rôle in the humid tropics than in the rest of the world. They are responsible for the decomposition of large amounts of soil organic matter and it has long been known that they take an active part in the destruction of cellulose in the soil. Certain fungal species form a symbiotic union with the roots of some plants and it has been shown, in the case of the European pine (*Pinus silvestris*), that satisfactory growth is never attained in the absence of these organisms:

such fungi are known as *Mycorrhiza*, and it has been claimed that some of them are able to effect nitrogen fixation.

Protozoa are unicellular, motile animals, represented in the soil by a large number of species: little attention was paid to their presence in the soil until Russell and Hutchinson¹ showed that they utilized bacteria as food, and suggested that, by setting a limit to bacterial activity, they diminished soil fertility. Although this view has not met with universal acceptance, it has been found that bacterial numbers in the soil vary inversely as the numbers of protozoa present.²

FACTORS AFFECTING THE ABUNDANCE OF MICRO-ORGANISMS IN THE SOIL

For agricultural purposes a soil is evaluated largely on the basis of the organic matter present and its rate of decomposition, and these factors are included in the rather vague term "fertility." The amount of organic matter present in a soil depends on its previous history and on the climatic factors, temperature, humidity and insolation: the rate of decomposition of soil organic matter is correlated with the concentration of micro-organisms present which, in turn, is conditioned by a number of factors, such as the size of the soil particles, degree of aeration, mineral constituents, soil reaction, moisture, temperature and the vegetation growing above the soil. Many of the factors affecting the numbers of bacteria present can be controlled, and it is of practical importance to consider precisely how these control the soil micro-flora.

(a) *Temperature*.—For all species of bacteria and fungi there is an optimum temperature which may differ considerably from one species to another. Although, as a general rule, fungi have an optimum temperature close to that of bacteria, they are able to withstand greater temperature ranges and to endure high temperatures for longer periods. Most species of micro-organisms have a temperature range between 10° and 45° C. and these are termed *mesophilic*: *thermophilic* organisms work at temperatures

above 45° and *psychrophilic* organisms are active between 5° and 30° C. The very few truly thermophilic bacterial species occur in the neighbourhood of hot springs. The optimum temperature for most species of soil micro-organisms lies between 25° and 37° C.

(b) *Soil moisture*.—The species of bacteria and fungi normally occurring in soil are not favoured by arid conditions but, during water-logging, the aerobic species suffer owing to insufficient aeration. The optimum degree of soil moisture for most aerobic species of micro-organisms appears to be somewhere between 50 and 70 *per cent.* of the saturation value: this is also the optimum value for the growth of vegetation.

(c) *Aeration*.—Most of the decompositions effected by micro-organisms in Malaysian soils are essentially oxidation processes requiring the presence of an adequate supply of free oxygen. The formation of nitrate from ammonia, whether by bacterial, chemical or photochemical means, can take place only in the presence of a sufficient supply of oxygen and if this supply is withheld the oxidation processes are inhibited.

(d) *Soil reaction*.—Species of micro-organisms are usually very sensitive regarding the reaction of the medium in which they live: normally an optimum *pH* value is found (certain species of yeasts have two or even three optimum *pH* values) and the *pH* range tolerated varies from one species to another. In temperate regions it is usual for the more acid soils to have a greater proportion of fungi to bacteria than is the case with less acid soils: this is not necessarily due to soil fungi having acidophilic characters, but is accounted for by the fungi having a much wider *pH* range than is usual with bacteria. The tropical soils of Malaysia are more acid than those of western Europe and North America, and have a high proportion of fungi to bacteria.

The "potato scab" of temperate regions, caused by *Actinomyces scabies*, will not develop if the soil reaction is more acid than *pH* 4.8, while *Plasmodiophora brassicae*,

the organism responsible for "club root" in cabbages, is eradicated when the pH value of the soil is raised to 7.2. In temperate countries, the nitrogen-fixing *Azotobacter* is rarely found in soils with a reaction more acid than pH 6 but it appears to be widely distributed in Malaysian soils, which normally have a more acid reaction.

(e) *Mineral content of the soil.*—Certain elements are necessary for the growth and reproduction of even the lowest forms of life, although it is surprising how bacteria and fungi will grow when it is evident that anything in the nature of nutrient can be present only in very small amount. Apart from carbon, hydrogen, nitrogen, oxygen, sulphur, phosphorus and potassium, the presence of minute amounts of other elements is essential; but in most cases these requirements can be satisfied by the traces present in water. It is improbable that the absence of certain essential metals ever sets a limit on bacterial activity in Malaysian soils.

(f) *Vegetation.*—The relation between the micro-flora of the soil and the vegetation growing above it is only an indirect one except in special cases, such as that of the nitrogen-fixing *Rhizobium* bacteria, which are associated with the formation of nodules on the roots of leguminous plants. In many cases the *Rhizobium* strains have proved to be specific, the organisms producing nodules on one plant species being unable to do so on other legumes. It has recently been shown that atmospheric nitrogen is fixed by bacteria living symbiotically in the root nodules of *Casuarina equisetifolia*.³

(g) *Depth.*—The concentration of micro-organisms in the soil varies inversely with the depth below the surface, but practically no organisms are found below the level to which soil humic matter has penetrated. In Malaysia, the depth of the top-soil is much less than in temperate countries: a considerable amount of local variation is found but, even in the virgin forest where a state of equilibrium has existed for centuries, when the carpet of partially decomposed leaves and twigs is removed, it is seen that the top-soil rarely extends for more than a few inches. When a top-

soil layer is encountered which can be measured in feet it is safe to conclude that the site was subject to water-logging at no remote date.

On many of the older rubber plantations, where the soil has been treated with but scant respect for a number of years, a top-soil layer hardly exists.

In Malaysia the maximum numbers of soil micro-organisms occur at a depth of one or two inches: the surface is not rich in life, doubtless on account of the sterilizing action of the sun. In Table VI are given some representative results obtained from plate counts of soil micro-organisms at varying depths.

TABLE VI

THE VARIATION IN NUMBERS OF MICRO-ORGANISMS WITH DEPTH IN THE MALAY PENINSULA

(a) Soil under primary forest.

Depth below surface in inches.	Numbers of micro-organisms per 1 g. moist soil.
0.5	420,000
3.5	443,000
8.5	142,000
11.0	51,000

(b) Soil under primary forest: the site was remarkable for the presence of earthworms (*Pontoscolex corethrurus*).

Depth below surface in inches.	Numbers of micro-organisms per 1 g. moist soil.
1.0	813,000
3.0	1,160,000
6.0	181,000
9.0	143,000

(c) Sungei Buloh Experiment Station: soil under a cover of *Centrosema pubescens*. On the block from which these samples were taken the top-soil was unusually deep, and it was known that the area had been water-logged before it was cleared of forest.

Depth below surface in inches.	Numbers of micro-organisms per 1 g. moist soil.
1.0	179,000
6.0	35,000
12.0	18,000
18.0	19,000



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THE NUMBERS OF MICRO-ORGANISMS IN THE SOIL

It has long been recognized that a relation exists between the micro-organic population of the soil and its fertility, and a certain amount of research work has been carried out on this subject during recent years. Several methods have been elaborated for the estimation of the total bacterial population in a sample of soil, but no one of these is entirely satisfactory; the results obtained by the different methods exhibit such considerable divergences that an estimate of the numbers of bacteria present in a soil sample is of no value unless it is known by which method it was determined.

The two most important methods in use for estimating the bacterial numbers in the soil are:—

(a) direct counting of the stained organisms under the microscope;

(b) the plate count method, in which the colonies developing on an agar plate as a result of inoculation of a given volume of soil suspension are enumerated.

The first method gives values many times greater than those obtained by the second procedure, but it is known that dead organisms are included in a direct count: on the other hand, the plate count method shows only colonies formed by aerobic micro-organisms able to grow on the particular type of medium employed. It has to be assumed that each colony on the plate represents a single organism in the inoculum, but it is generally recognized that this assumption is rather wide of the mark.⁴ Nitrifying organisms, *Azotobacter*, *Rhizobium* and obligate anaerobes are not determined in the usual plate count method.

As a routine method of estimating the actual numbers of micro-organisms in soil the plate count method has not been surpassed and its reliability has been investigated by Fisher, Thornton and Mackenzie,⁵ and by Waksman.⁶ Nevertheless, certain drawbacks are inherent in both methods. The direct count method is hardly suitable when large numbers of determinations have to be made,

and the uncertainty of the significance of the results is such that it is rarely employed in agricultural work. The plate count method is tedious and it is essential that the platings be carried out in replicate: a few isolated results are valueless and may be misleading. By the use of Thornton's medium,⁷ the growth of bacteria is encouraged at the expense of the fungi, but not infrequently the whole of a plate may be covered with a fungoid growth which prevents accurate counting of the bacterial colonies present.

In temperate regions it is customary to enumerate only the bacteria and to ignore the presence of fungi, or to employ a special plating medium if it is desired to enumerate the latter. In the humid tropical regions, however, fungi predominate over bacteria to such an extent that, even by the use of Thornton's medium, it is impossible to obtain plates free from fungi. Actually, fungi play such an important rôle in effecting the decomposition of the soil organic matter in the humid tropics, that any determinations of the soil micro-organisms which failed to take them into account would be misleading.

In Europe and North America the numbers of bacteria per gram of soil, as found by the plate count method, vary between several thousands and some millions, but almost all determinations have been carried out on cultivated soils. Having regard to the abundant native flora and fauna of Malaysia it might be anticipated that the soil would harbour a rich micro-flora, but this is not realized in practice. A study of the concentration of micro-organisms in the soil in the Malay Peninsula has shown that the numbers are surprisingly constant, having a value of about 500,000 micro-organisms per 1 gram of moist soil. Almost invariably fungi predominate over bacteria and the results show no significant difference between the numbers present in cleared land and in soil under primary forest, suggesting that the fluctuations observed in bacterial numbers in the soils of temperate regions are largely reflections of changes in temperature and soil moisture content.⁸

An experiment was carried out in which the numbers of soil micro-organisms were determined, by the plate count

method, at approximately weekly intervals on a block at the Rubber Research Institute Experiment Station in Selangor. Counts were made while the block was still under forest and were continued during the processes of forest clearing, "burning-off," and planting with rubber seedlings and a leguminous cover. The experiment was continued for two years and the numbers of micro-organisms showed significant differences from the value of 500,000 only during the course of "burning-off" operations, when the soil was impregnated with wood ash. That the increased population was attributable to the presence of the alkaline wood ash and not to any "partial sterilization" effects is certain.

On a few sites in the Malay Peninsula, such as in peat areas and in mangrove swamps, low counts were obtained; but such results would be anticipated where the usual aerobic conditions are lacking. Anaerobic micro-organisms are rarely found in forest and cultivated soils in Malaysia.

Previously it had been assumed that removal of the forest cover resulted in an increased microbiological population of the soil as a consequence of the increased soil temperature; it is now known that such is not the case and the question of the chemical and bacteriological effects of clearing forest is discussed on page 103.

BACTERIA

All bacteria are microscopic in size and may be classed as coccoid (i.e. spherical), rod-shaped or spiral-shaped. Although all bacteria exhibit a certain degree of variation with regard to shape and size, such differences are not usually considerable so that information concerning the dimensions of a species is often an aid to its identity. An average rod-shaped organism is about 0.5μ in breadth and from 3 to 4μ in length, μ being the symbol for the *micron* which is $1/1000$ mm. or about $1/25000$ inch.

The variation in form shown by some species of bacteria has rendered their classification a matter of difficulty and uncertainty. With young cultures of some species, not only is a certain amount of individual variation apparent but,

perhaps, all the organisms present may exist either as rods or cocci, according to the conditions which obtain. A Malayan species of *Hevea* latex bacteria, *Micrococcus chersonesia* Cbt., was found first as a coccus, but it gradually changed to a rod form; subsequent plating resulted in the reappearance of the coccus form which again reverted to the rod form, but eventually the culture lost this power of transformation and the rod form persisted. Such variation is termed *pleomorphism* or *dissociation*. With old cultures, large aberrant forms may be present and, on occasion, hardly two of the organisms are alike: such are known as *involution* forms. The variation in bacteria is frequently ill-defined and some confusion exists with regard to the nomenclature of the subject: it seems more than probable, however, that the nature of the variation is similar to that exhibited by macro-organisms, a certain amount of true variability being associated with a young and vigorous culture, while the appearance of large and bizarre involution forms in old cultures has a parallel in the tendency shown by old species (in the phylogenetic sense), such as the Proboscidea (elephants), for individuals to become fewer and larger.

Although the subject has not yet been investigated very thoroughly, it appears that the life cycles of bacteria are usually relatively simple, showing none of the complex transformations exhibited by many microscopic animals. With some species, notably *Rhizobium leguminosarum*, the life cycle is highly complicated and the organism passes through a number of different stages.⁹

Reproduction is achieved by a process of cell division, a single unit dividing into two and thus giving rise to two daughter cells which further divide and so on. Given favourable circumstances the generation time may be as brief as 15 minutes. There is some evidence to show that union of two cells may occur at rare intervals.

Structure of Bacteria

A biological cell comprises a nucleus, a semi-fluid material, largely protein in nature and known as *cytoplasm*, and the

cell membrane. Until recently no convincing proof had been submitted of the presence of a nucleus in bacteria but, by means of a new staining technique, Stoughton¹⁰ has now demonstrated the existence of what appears to be nuclear structures in the plant pathogens *Phytophthora malvacearum* Erw. Smith. The cell membrane is a protective covering secreted by the cytoplasm and behaves as a semi-permeable membrane through which liquid food and waste products pass. Some bacteria have also a gelatinous covering and it is on account of the mucilaginous nature of this *capsule* that cells of certain species cohere to form a slimy mass known as *zooglyæa*. Locomotion is achieved by the movement of fine cilia situated on the cell wall and termed *flagella*, but not all species of bacteria are motile.

Spore formation takes place in some species whereby the organisms are enabled to survive adverse conditions, such as heat and desiccation: in sporulation the cell shrinks and becomes covered with a hard film formed from a secretion of the cytoplasm. In spore-forming organisms, an *endospore* is present in the normal cell and, in some species, becomes greatly enlarged at the expense of the rest of the cell when sporulation occurs.

Destruction of bacteria is effected by methods of sterilization and disinfection; the former term denoting the total destruction of all organisms present, while the latter usually applies only to the elimination of disease-bearing species. Sterilization is effected by the action of heat or chemicals: spore-forming organisms are more difficult to destroy on account of their increased power of resistance. It has been shown that the course of the death of bacteria by disinfection processes follows the monomolecular law:

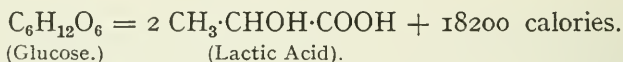
$$-dy/dt = ky,$$

where y represents the number of organisms surviving at time t and k is a constant.¹¹ That is to say, the rate of death is proportional to the number of surviving organisms. This decrease in numbers of bacteria as a result of exposure to adverse conditions follows the usual equation representing the phase of decline in the normal bacterial growth curve (see page 62).

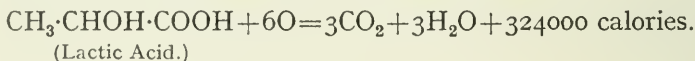
Bacterial Metabolism

The possession of chlorophyll by green plants enables them to utilize energy in sunlight and so effect the elaboration of complex organic substances from carbon dioxide, water, and simple nitrogen salts absorbed by the root system. Animals obtain energy by chemical decomposition of complex organic materials into simple substances, and bacteria and fungi, lacking chlorophyll, also derive the energy necessary for growth and reproduction entirely from chemical sources. The vast majority of species of bacteria and fungi obtain carbon and nitrogen from complex substances elaborated by plants and animals.

The chemical action by bacteria on certain groups of compounds has been studied in detail and these reactions often afford a ready aid to identification. Sugars are readily decomposed by most species of bacteria, giving rise to organic acids, alcohols, carbon dioxide and other compounds, and such fermentations are accompanied by the liberation of energy. The disruption of glucose to lactic acid, for example, results in the liberation of 18200 calories per 1 g.-molecule of glucose:

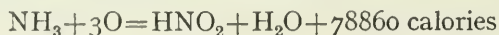


The oxidation of lactic acid to carbon dioxide and water is accompanied by the release of 324000 calories:

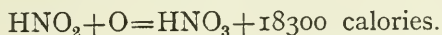


Many complex carbohydrates are subject to attack by bacteria, with the production of varied products of decomposition. As a rule, amino acids and proteins are readily disrupted by bacteria and a variety of compounds appear, although ammonia and fatty acids are frequently the final products of the reaction.

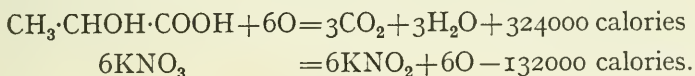
The oxidation of ammonia to nitrous acid by *Nitrosomonas* takes place according to the equation:



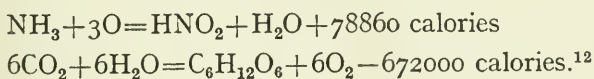
and this balance of 78860 calories per 1 g.-molecule of ammonia is utilized by the micro-organisms responsible for the change. In the same way, *Nitrobacter* can oxidize nitrous acid to nitric acid according to the scheme:



Some oxidation processes can be effected in the absence of air, the oxygen required being taken from a suitable oxygenated compound present. Thus the oxygen necessary for the oxidation of lactic acid may be obtained by the reduction of nitrate according to the reactions given below, which result in a gain in energy of $(324000 - 132000) = 192000$ calories per 1 g.-molecule of lactic acid decomposed:



Some bacteria can obtain carbon from carbon dioxide and such is the case with the nitrifying organisms. With *Nitrosomonas*, for instance, the energy released by the oxidation of ammonia to nitrous acid is utilized in the synthesis of glucose from carbon dioxide:



Enzymes

The chemical reactions effected by bacteria are brought about by means of enzymes which are present in, or on the surface of, the bacterial cells. The precise nature of enzymes is still obscure but, in general, they may be regarded as somewhat unstable catalysts which are able to effect the decomposition of complex organic substances: a small amount of enzyme may be responsible for the transformation of large quantities of material. In most cases, enzymes appear to be specific in their actions; thus cellulose can be decomposed by the enzyme *cellulase* but not by *lactase*, the enzyme responsible for the oxidation of lactic acid. Protein hydrolysis is effected by a class of enzymes termed *proteases*.

Classification of Bacteria

The classification of bacteria is a question of difficulty particularly as some species can occur both as rods and as cocci. The most satisfactory classification yet evolved is that of Bergey and the American Society of Bacteriologists.¹³ Bacteria are classified not only according to their morphological characters, such as shape, presence or absence of endospores, motility, etc., but also on the basis of their behaviour with certain chemicals and stains. In general, bacteria are arranged in orders and families on account of morphological characters and in genera and species according to their chemical activities.

Bergey's scheme of classification is considered in the appendix in so far as commonly occurring soil bacteria are concerned.

FUNGI

Fungi are multicellular plants which resemble bacteria in that they lack chlorophyll and so are unable to affect the formation of cell material by the process of photosynthesis: the energy for growth and reproduction is obtained by the disintegration of substances of high energy content to compounds of low energy value. The fungi are composed of vegetative (or assimilative) and reproductive cells; the fungus body (or *thallus*) comprises a number of thread-like *hyphae*, usually branching to give a network of *mycelium*. In the higher fungi (Ascomycetes and Basidiomycetes) the hyphae are divided into cells of variable length by transverse membranes known as *septa*; the lower fungi (Phycomycetes) are non-septate.

Reproduction is effected by spores and the process of spore formation may be asexual or sexual. Asexual spore production occurs in all fungi, while sexual spores are found mainly in the Phycomycetes. Asexual reproduction can take place according to two different processes:—

(a) *Endospores* result from division of the protoplasm within a mother-cell, when the encasing cell is termed a *sporangium*, and the hyphae bearing the sporangia are known as *sporangiophores*;

(b) A *conidium* is a single cell formed at the tip of a hypha, which latter is then termed a *conidiophore*. Frequently one conidium is formed after another on the same hypha, so that a chain of spores results.

Although fungi are of considerable importance in the soil, and more so in humid tropical regions than in temperate zones, comparatively little is known regarding tropical soil fungi. Fungi play an important part in the decomposition of soil organic matter, and their multiplication in the soil results in the immobilization of a certain amount of plant nutrient material. In the soils of Malaysia, fungi predominate over bacteria and, taking into consideration the fact that each individual fungus occupies a much greater volume than does a single bacterial cell, it is evident that a considerable proportion of the total volume of micro-organisms present in such soils consists of fungal material.¹⁴

Classification of Fungi

The classification of fungi is based on the presence or absence of septa, the structure of the asexual fruiting bodies and the nature of sexual reproduction, when this method is present. A classification scheme is briefly considered in the appendix.

Waksman¹⁵ investigated the soil fungi and examined soil samples from various localities in North America and from Alaska and the Hawaiian Islands and found certain species to be widely distributed. The Mucorineae, and to a lesser extent the *Penicillium*, are more largely represented in cooler climates while *Aspergillus* is more abundant in warmer regions. *Trichoderma* species are found extensively in the more acid and water-logged soils.

PROTOZOA

Although protozoa occur in the soil in some numbers their functions are not yet completely understood: many feed on living bacteria, while others are able to utilize organic and inorganic materials in the soil. The unicellular Protozoa are divided into four classes: the Sarcodina,

Mastigophora and Infusoria are differentiated according to their locomotory organs and all are represented by species occurring in the soil, while the Sporozoa, typified by the malaria parasite, are parasitic and without organs of locomotion.¹⁶

If, as has been surmised, the intestinal protozoa found in wood-destroying termites are able to fix atmospheric nitrogen, the importance of these creatures in tropical soils may be considerable.¹⁷

SUMMARY

The most important groups of soil micro-organisms are bacteria, fungi and protozoa and, in soils in temperate regions, bacteria occur in greatest numbers while fungi predominate in the soils of the equatorial belt.

In general, the number of soil micro-organisms present depends on temperature, moisture, aeration, soil reaction and depth, there being an optimum for each of these factors. In Malaysia, however, conditions are very uniform and the concentration of soil micro-organisms (as determined by the plate count method) is constant under all usual aerobic conditions.

Anaerobic micro-organisms are rarely found in Malayan soils except under swamp conditions.

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V. THE BACTERIAL GROWTH CURVE

WHEN a few bacteria, in pure culture, are introduced into a nutrient medium suitable for their growth and reproduction there is, at first, a rapid increase in population which is followed by a slow decline in numbers until, finally, the whole colony is extinct. The curve obtained by plotting the population at any instant against the time elapsed throughout the life of the colony conforms to a general type, of which an example is given in Fig. 3, provided that the temperature is maintained constant and there is no contamination from external sources.

It is evident that no one simple equation can be found to express a skew curve of this nature, but the curve admits of division into a number of fairly well-defined portions. Writers are by no means agreed on the division and nomenclature of the phases constituting these growth curves and, for the present purpose, we shall follow Topley and Wilson,¹ who recognize four growth phases:—

- (a) lag phase (*A-B* in Fig. 3) ;
- (b) logarithmic phase (*B-C* in Fig. 3) ;
- (c) stationary phase (*C-D* in Fig. 3) ;
- (d) phase of decline (*D-E* in Fig. 3).

In a general way, the growth phases mentioned can be recognized in all bacterial growth curves but, in some cases, the lag phase is of very brief duration, and the decline phase admits of further subdivision.² It is a matter of interest that the appearance of the phase of decline is not necessarily the result of a deficiency in the food supply, but, in the case of bacteria, it may be due to the presence of inhibitory products of metabolism.

During the lag phase, the duration of which varies considerably, the organism is becoming inured to a new set of conditions; in the illustration given in Fig. 3 this phase

occupies but a small portion of the whole curve. Once an organism has adapted itself to altered conditions a rapid rise in the population takes place, and the logarithmic phase is remarkable chiefly for the great increase in numbers in a relatively short space of time. During this growth phase, the rate of increase of bacteria at any instant varies directly as the number of organisms present and can be represented by the equation:

$$db/dt = kb,$$

where b is the number of micro-organisms present at time t and k is a constant. The relationship may also be expressed:

$$b = Ae^{kt},$$

where e is the base of natural logarithms and equal to 2.718, A is a constant and b , t and k have the same significance as before.

It appears to be the rule that the stationary phase, during which the population remains approximately constant, is relatively of very short duration. The phase of decline occupies a comparatively large portion of the whole growth curve, as the rate of decrease is usually slow compared with the rapid rise in population characteristic of the logarithmic phase. The phase of decline is also logarithmic, and can be expressed by the equation:

$$-db/dt = k'b$$

or

$$b = Ae^{k't},$$

where the symbols have the same significance as before. It is well known that, in the presence of disinfectants, the death rate of bacteria is a function of the number of cells surviving, and the ultimate process of extinction may be very slow indeed (see page 55). It is sometimes a matter of difficulty to define growth phases accurately and, in general, the transition from one phase to another is abrupt and not gradual.

THE RISE AND FALL IN POPULATIONS

It seems evident that the laws which regulate the rise and fall of bacterial populations are of very general application,

for it is difficult to believe that the growth of populations of higher plants and animals is not governed by the same laws.³ It is not always easy to measure changes in plant and animal populations over lengthy periods; but the data available support the suggestion that a biological population which can be regarded as being maintained in a closed system at a constant temperature first increases and then declines in numbers according to the laws expressed in the bacterial growth curve.

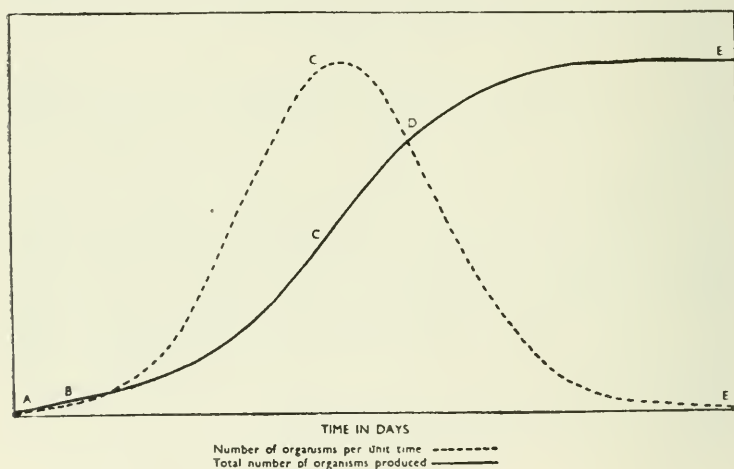


FIG. 3. THE GROWTH OF A POPULATION OF YEAST CELLS.
(Carlson's Data.)

The full line represents the summation curve showing the total number of organisms produced during the experiment. The dotted line is the usual bacterial growth curve and depicts the number of living organisms present at any given time.

In both curves *A-B* represents the lag phase, *B-C* the logarithmic increase phase, *C-D* the stationary phase, and *D-E* the phase of decline.

Here must be mentioned a point frequently overlooked when comparisons are made between populations of higher plants and animals and those of micro-organisms. The numbers of bacteria in a culture medium are usually determined by counting the cells present, in the same way that measurements of animal populations may be made by

counting heads, but when the strength of a colony is estimated by measurement of some accumulating product of metabolism, such as carbon dioxide or nitrate (to which contributions have been made by organisms both living and dead), what is being evaluated is not the actual population at the time of measurement but the total numbers (living and dead) which have existed since the foundation of the colony. The plot of the total number of organisms which have

TABLE VII
GROWTH OF A POPULATION OF YEAST CELLS (CARLSON'S DATA)

Days of growth.	Daily growth of yeast.	Total quantity of yeast.
0	—	9.6
1	8.7	18.3
2	10.7	29.0
3	18.2	47.2
4	23.9	71.1
5	48.0	119.1
6	55.5	174.6
7	82.7	257.3
8	93.4	350.7
9	90.3	441.0
10	72.3	513.3
11	46.4	559.7
12	35.1	594.8
13	34.6	629.4
14	11.4	640.8
15	10.3	651.1
16	4.8	655.9
17	3.7	659.6
18	2.2	661.8

During the logarithmic phase (2nd to 7th day) and the phase of decline (9th to 17th day), the plot of the time against the logarithm of the daily growth is a straight line.

existed in a microbial colony against the times elapsed, gives a summation curve of which an example is shown in Fig. 3. This corresponds to the bacterial growth curve depicted in the same figure, and the data from which these two curves are constructed are given in Table VII. In the same way the plot of the total number of trees killed by a fungus epidemic, and the growth of rubber fruits after

pollination, to take illustrations at random, are examples of summation curves. Such can be transposed to ordinary growth curves by plotting the numbers of trees killed or the fruit growth in unit intervals of time against the time elapsed.

It seems highly probable that when a species of plant or animal is introduced into a new habitat, its initial rise and subsequent decline in population follow the bacterial growth curve, for the restrictions of a closed system and a constant temperature usually apply. Many species reaching new lands in which climatic conditions are suitable for them, find themselves unable to compete successfully with the native population and so never gain a footing; but once a species has become established, although certain local and seasonal fluctuations in population may occur, there is little doubt that, under natural conditions, the whole history of the introduced species closely conforms to the bacterial growth curve. When an organism is introduced into a new habitat it seems possible that the duration of the lag phase depends primarily on the phase of the organism in its former habitat. A species in the logarithmic phase will exhibit a much curtailed lag phase in new surroundings compared with that shown by a species formerly in the decline phase.

BIOTIC POTENTIAL AND ENVIRONMENTAL RESISTANCE

It is interesting to consider why, under conditions of a closed system and a constant temperature, all populations (bacterial, plant or animal) do not continue indefinitely along the logarithmic phase of increase. Doubtless, this phase is terminated for different reasons with different species but, in general terms, the explanation appears to be as follows. A plant or animal appearing in a new faunistic region may encounter conditions differing considerably from those obtaining in its original habitat. The immigrant species may possess a certain degree of adaptability or plasticity and may be able to change its mode of life to meet the altered circumstances. If the degree of

adaptability is small the chances are heavily against the species becoming established in its new surroundings.

It has been pointed out³ that a distinction may be drawn between species of plants and animals which are phylogenetically "old" and "young," the latter being those which are in the phase of increase in the habitat under consideration, while the former are those which have passed the stationary phase and are declining in numbers. Certain characteristics are associated with this age distinction; in general, in an "old" species the geographical races exhibit definite and constant differences and individual variation is slight, while a "young" species is characterized by slight geographical but marked individual variation. With Malaysian butterflies it has been found, as far as tested, that when there is a great preponderance of males to females, usually the other characteristics are those associated with species in the phase of decline.

It is evident that, during the logarithmic phase, organisms possess a degree of adaptability which is gradually lost as the species proceeds along the road to stability and then on to decline and decay; at the same time, conditions prevailing in the habitat are gradually changing, and these will demand adaptations in the organisms. The power of adaptability possessed by an organism and the continuous alterations in the habitat correspond to the terms *biotic potential* and *environmental resistance* respectively employed by Chapman,⁴ who supposes that equilibrium is attained when

$$B = R,$$

where B represents the biotic potential and R is the environmental resistance.

During the declining stages in the life of a species, not infrequently, a comparatively large amount of the total life mass is concentrated in a few individuals. The dying species of *Rhinoceros* are large and bulky and comparatively few in numbers, so that the loss of a few individuals has important effects on the future racial history. The formation of the curious, enlarged involution forms of bacterial cells found in old cultures appears to be a parallel case.

PESTS AND DISEASES

Instances of the general applicability of the bacterial growth curve are very frequently encountered in the equatorial regions, where life cycles proceed at a much greater speed than in temperate countries.

It has been shown that the incidence of *Fomes lignosus* on rubber estates, if uncontrolled, follows a curve of the type under consideration. During the initial stages of infection the spread of the disease may be slow, but this is followed by the increase phase when growth is rapid; latterly, as the biotic potential of the causal organism falls off, the decline phase is entered and finally the disease almost, if not entirely, disappears. Rarely is treatment accorded in the early and more virulent stages of the disease, but when control measures are set in train during the phase of decrease it is, of course, debatable how much of the final success can be fairly attributed to the treatment! It is not generally realized, perhaps, that all bacterial and fungal diseases and plant and animal pests are more amenable to control at some phases than at others. The correct time to apply remedial measures is during the initial lag phase, but such a counsel of perfection is rarely within the bounds of practical politics. Once the initial stage has been passed and the disease-bearing organism has become established in a new habitat, the difficulty of eradication is increased although, of course, the logarithmic phase of increase can usually be curtailed by treatment. Mycological experiments rarely take these considerations into account, so that it is hardly surprising that treatment for specific diseases is found to be much more efficacious in some cases than in others.

There is little doubt that the outbreak of an insect pest is governed by the same considerations.

SUMMARY

When bacteria are grown in pure strain at a constant temperature, after an initial lag period of variable duration, there is a rapid increase in the population until, following a

brief stationary phase, the numbers decline until the whole colony becomes extinct. Relative abundance and marked individual variability are associated with the increase phase, in contrast to the lesser numbers and diminished variation characteristic of the decline phase.

It appears that plant and animal populations follow these same growth laws, under conditions of a constant mean annual temperature and a closed system. The sudden appearance and gradual decline of pests and diseases on plantations are illustrative of the same laws.

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Phase of adjustment (=Topley and Wilson's lag phase),
Phase of increase (=Topley and Wilson's logarithmic phase),
Phase of crisis (=Topley and Wilson's stationary phase),
Phase of decrease (=Topley and Wilson's phase of decline), and
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VI. THE SOIL ORGANIC MATTER

THE soil particles are composed of water, mineral salts and organic matter, but the customary method of examining soil in the laboratory is concerned with determination of the moisture content and with mechanical and chemical analyses. In ordinary analysis, the moisture is found by estimation of the loss in weight, after drying at a temperature slightly above the boiling point of water for some hours; for a very rough and ready measure of the organic matter content may be taken the loss on ignition, after correction for the moisture present.

The method of MECHANICAL ANALYSIS is concerned with the *size* of the soil particles, and consists of separating the mineral portion of the soil into fractions according to the diameter of the particles. A knowledge of the texture of the soil is of value to the agriculturist, but the information acquired as a result of mechanical analysis is frequently out of proportion to the labour entailed.

Of the soil fractions, clay is by far the most important and it alone is chemically reactive. Essentially, clay is an aluminosilicic acid of complex composition: it is a colloid and has the power of adsorbing certain electro-positive ions to form a loose complex. Metal ions thus held by clay particles can be replaced by other ions of a basic nature and the whole process, which is largely a surface phenomenon, is known as *base exchange*. Certain of the physical properties of clay, such as power of retaining water, stickiness and capacity to swell or shrink according to the moisture content, have an important bearing on the question of soil fertility.

Base-adsorbing powers are possessed also by humus which, weight for weight, are more important than those of clay.¹

Chemical analyses of soil are concerned primarily with measurements of nitrogen, potassium and of phosphorus as phosphate—in fact, with the elements which may prove

to be limiting factors in crop production—but it is evident that, in the humid tropics, the mineral portion of the soil is of considerable importance as its rate of decomposition may be increased by cultural operations.

It is the presence of organic matter which differentiates soil from other naturally occurring, finely powdered materials, such as sand, and usually the fertility of the soil is intimately connected with its organic matter content.

Under conditions of equilibrium, such as exist in the forests of Malaysia, and in fact under all natural conditions where no additions of organic material are made in the form of fertilizers, the soil organic matter is almost entirely derived from the vegetation which covers the forest floor. The excreta and dead bodies of animals add their quota, but this contribution is small compared with that obtained from the vegetation.

THE DECOMPOSITION OF SOIL ORGANIC MATTER

The Chemical Composition of Plants

The principal constituents of plants are cellulose, hemicelluloses, lignin, proteins, simple carbohydrates (sugars and starch), fats, waxes, oils, gums and mineral salts. The chemical composition of plants varies according to age and species: as a plant grows the proportion of cellulose and lignin increases considerably, while the amount of protein and water-soluble material decreases. Some plants contain very characteristic substances such as alkaloids, latex, etc., of quite different chemical composition, so it would not be anticipated that all plants would decay to give a product of definite and constant composition.

Regarding the formation of soil organic matter the *water-soluble substances* present in plants (simple carbohydrates such as glucose and fructose, amino acids and nitrogen-free organic acids) are of minor importance, as they are rapidly decomposed by the soil micro-organisms and so take no part in the formation of soil humic matter. *Cellulose* is a condensation product of glucose, insoluble

in water and not resolved by dilute acids, and is the chief constituent of fibrous and woody portions of plants; materials such as flax and hemp are largely composed of pure cellulose. In the soil, in temperate regions, cellulose decomposition is effected by the agency of aerobic and anaerobic bacteria, actinomyces and fungi, but, in the acid soils of the humid tropics, it is probable that fungi and termites are mainly responsible for the disruption of cellulose. The destruction of cellulose by animals may be due to the presence of intestinal enzymes or it may be effected by bacteria or protozoa in the digestive tract.² The *hemicelluloses* are condensation products of simple carbohydrates (hexoses and pentoses) with uronic acid compounds such as pectin; all hemicelluloses are hydrolysed by dilute mineral acids, yielding hexoses and pentoses, and are readily decomposed by soil micro-organisms.

The chemical nature of *lignin* is not yet fully understood³; it is known that this substance contains aldehyde, hydroxyl and methoxyl groupings and the presence of the last-named has been utilized for the quantitative estimation of lignin. Lignin enters into some kind of association with cellulose and, in this form, occurs in the tissues of the growing plant; in the soil it is decomposed but slowly and so tends to accumulate.

The most important nitrogen compounds in the plant are *proteins*, substances composed of chains of amino acids and differing considerably from one another in their resistance to attack by micro-organisms. The simple amino acids such as glycine, $\text{CH}_2(\text{NH}_2)\cdot\text{COOH}$, and aspartic acid, $\text{HOOC}\cdot\text{CH}_2\cdot\text{CH}(\text{NH}_2)\cdot\text{COOH}$, readily undergo decomposition with formation of a variety of simple compounds such as ammonia, organic acids and alcohol. Pure proteins contain about 15 to 19 *per cent.* of nitrogen and, in the laboratory, their estimation is carried out by heating with sulphuric acid, collection of ammonia thus formed and multiplication of the nitrogen figure obtained from the ammonia determination by 6.25.

The remaining plant constituents, such as fats, waxes and oils which are esters of alcohols and higher fatty acids,

are of small importance in the formation of soil organic matter under normal aerobic conditions. Cellulose, lignin and pentosans (the most commonly occurring hemicelluloses) constitute between seventy and eighty *per cent.* of the total plant substances.

The Composition of Soil Organic Matter

Some confusion exists with regard to the nomenclature employed by different authors for the soil constituents. It is, perhaps, rather misleading to speak of "soil constituents," for the soil organic matter must be considered as being divisible into groups of related substances rather than as comprising a number of well-defined chemical entities. The total organic matter in the soil is referred to as the *soil organic matter*: the dark-coloured, colloidal organic matter, characteristic of the soil, is termed *humic matter*, while the remaining colourless organic material, which is largely soluble, and the undecomposed parts of plant and animal residues are regarded as the *non-humic matter*.

The different groups of the organic constituents of the soil decompose at different rates, so there is an accumulation of the most resistant materials. Between seventy and eighty *per cent.* of the soil organic matter consists essentially of a dark-coloured, colloidal complex of lignin and protein which undergoes disintegration very slowly.^{4,5} The exact nature of the union between these substances (or groups of substances) is not known, but evidently the combination is a very intimate one. It has been shown that protein substances which are readily decomposed by bacteria become resistant to the action of micro-organisms in presence of lignin.⁶ Lignin contains no nitrogen so that, essentially, the soil humic matter consists of nitrogen-free lignin and the nitrogen-containing protein complex. Humic matter, obtained from different types of soils receiving different manurial treatments, is remarkably uniform in general properties but, nevertheless, its constitution varies between fairly wide limits.

The slow disintegration of the ligno-protein complex in the soil is effected by bacteria and actinomycetes, and also by some species of higher fungi (Hymenomycetes).

The colourless non-humic matter forms a comparatively small proportion of the total soil organic matter and the greater part of the nitrogen present in this group occurs in the form of peptides.

In moist soils, fats are slowly decomposed but, in dry soil, decomposition may be inhibited altogether; waxes are even more resistant to microbiological attack. It has been suggested that soil exhaustion may be due to an accumulation of fats and waxes,⁷ but, although this view has not been generally accepted, it may well be that decomposition of some of the soil humic matter is delayed owing to a coating of fats and waxes on the soil particles. It is well known that increased bacterial activity follows treatment of soil by fat solvents, such as chloroform; in Table VIII is shown the result of extracting a Malayan soil with chloroform for several days.

TABLE VIII
INCREASE IN MICROBIOLOGICAL ACTIVITY AS A RESULT OF EXTRACTION
OF SOIL WITH CHLOROFORM

	<i>F</i> (mg. CO ₂ per 100 g. of soil per day).
Before extraction with chloroform	11.3
After extraction with chloroform	14.3

The Carbon : Nitrogen Ratio

The course and speed of the decomposition in the soil of such materials as cellulose, hemicelluloses and the ligno-protein complexes, are influenced by the carbon/nitrogen ratio. With most cultivated soils this ratio approaches a value of 11 but, clearly, it depends on the relation between temperature and rate of decomposition of plant residues. In arctic regions, where the soil contains much undecomposed vegetation, the C/N ratio is necessarily higher than in the

equatorial belt where decomposition of all plant and animal remains is rapid. There is a definite C/N ratio in the material constituting microbial cells, so that the presence of a certain amount of nitrogen is essential for growth and reproduction of micro-organisms, and in the complete absence of this element no biological decomposition can take place. In organic materials any nitrogen present in excess of the requirements of the micro-organisms effecting the decomposition appears finally as ammonia or nitrate or both; with a deficiency of this element decomposition is retarded, perhaps even inhibited.⁸ It is well established that the addition to the soil of a simple carbohydrate, such as glucose, is followed by the disappearance of any nitrate present. The explanation of this is that, although glucose constitutes a readily available source of energy for micro-organisms, growth can take place only if sufficient nitrogen is present. In the soil the most readily available nitrogen occurs in the form of nitrates, so these compounds are utilized immediately by the organisms to make good the nitrogen deficiency during the disruption of the carbohydrate.

This immobilization of the soil nitrogen, consequent upon the addition of a substance such as glucose, is quite temporary and the nitrogen is returned to the soil in due course as the micro-organisms perish and suffer decomposition by their fellows. The transitory nature of the phenomenon is apt to be overlooked and in perennial crops, such as rubber and coconuts, such an immobilization process is not without advantages. Another case in point is the rotting of timber, where the C/N ratio is very high, and for the decomposition to proceed apace, whether by the agency of termites or of micro-organisms, reserves of nitrogen must be present. Any nitrogen used may remain locked up for a considerable period, but it will be returned to the soil ultimately. In tropical Malaysia, the rotting of timber in the forest is effected very largely by the agency of termites; little is known concerning the metabolism of these insects, but it appears that the cellulose in timber may be decomposed while the lignin remains almost unaltered.⁹

PEAT

Peat formation results when the soil organic matter decomposes in the absence of adequate supplies of oxygen. Such conditions obtain with water-logging, when the activities of aerobic species of bacteria and fungi are inhibited and decomposition is effected by anaerobic organisms. Disruption under anaerobic conditions is much slower than the usual aerobic process.

In the normal course of events on the lowlands of Malaysia there is very little accumulation of organic matter in the soil, for humus decomposition takes place as fast as humus formation. Peat beds evidently represent an accumulation of organic matter and it was formerly thought that such could not occur in equatorial regions. According to Mohr,¹⁰ peat formation can take place only in the absence of calcium, when the acids formed as a result of cellulose disintegration are not removed, but gradually accumulate and so cause a slowing down in microbiological activity. In the presence of lime, the calcium salts of the acids are formed and many of these are precipitated and so removed from solution.

In Java, true peat is found only in the lime-deficient soils of Bantam, but along the east coast of Sumatra and the west coast of the Malay Peninsula are considerable areas of peat. Peat soil from the Malayan coastal belt has been examined by Dennett¹¹ who found the moisture content to be about 80 *per cent.* and 80 *per cent.* of the dry matter to be organic in nature; the *pH* value is about 3.0 or below. Deposits of peat occur on some of the Malayan hills, notably on Gunong Batu Brinchang at an elevation of from 5000 to 5500 feet.

The nature of peat varies considerably with the vegetation from which it originated and, in temperate regions, peat soils can be classified according to the vegetation growing above them: in Malaysia it is out of the question to attempt any such classification with the data at present available. Peat contains a considerable proportion of water and marked shrinkage occurs on drying, with consequent drop in the level of the soil. This is demonstrated on several rubber

plantations in west Selangor where drainage methods have been applied to peat soils and the ensuing soil shrinkage has caused the trees to keel over owing to insufficient support to the root system. On peat areas in Malaya, permanent crops usually thrive during their early stages, but subsequently they are apt to become sickly; if peat is thoroughly drained before planting, it shrinks to a dry powder which cannot be reconditioned.¹¹

Waksman and Purvis¹² have found that peat usually has an abundant anaerobic micro-flora which *increases* with depth, and the rate of decomposition is profoundly affected by the moisture content. In a sample of lowmoor peat examined by these authors, it was found that the peat decomposed as a whole without any chemical complexes disappearing more rapidly than others, indicating that a condition of equilibrium had been attained. A tendency was noticed, however, for the rather more rapid disappearance of the non-nitrogenous complexes leading to an increase in the nitrogen content of the residual peat. Drying of peat, followed by remoistening, resulted in an increased speed of disintegration.

Peat soils in Malaysia are remarkable for the almost complete absence of aerobic bacteria and the very sparse population of aerobic fungi.

On plantations in Malaysia, the water in ditches draining peat areas is always of a deep reddish-brown colour, as water percolating through soil rich in organic matter is able to dissolve iron salts, and a portion of the iron is subsequently precipitated as dark reddish-brown ferric hydroxide. A number of thread-like bacteria (appertaining to the so-called "higher bacteria"), of which the best known is *Crenothrix*, are found in these iron-containing waters and deposit iron oxide as a product of their metabolism.

THE EVOLUTION OF CARBON DIOXIDE AS AN INDEX OF SOIL MICROBIOLOGICAL ACTIVITY

The final products of decomposition of the soil organic matter are carbon dioxide, ammonia and water. Almost

all the carbon dioxide evolved results from the activities of soil micro-organisms, although on calcareous soils a small amount may be attributable to the destruction of mineral carbonate by organic acids. This suggests that a measure of the microbiological activity of the soil might be obtained by determination of the carbon dioxide or ammonia liberated; in actual practice, ammonia formation can be assessed only with difficulty on account of the possibility of part of it having been oxidized to nitrite and nitrate by biological or other means.

The idea of following the course of the decomposition of soil organic matter, or of estimating the soil microbiological activity, by laboratory measurement of the carbon dioxide evolved seems to have originated with Kissling and Fleischer,¹³ but the subject has been examined in some detail by Lemmermann and Weissmann,¹⁴ and by the writer.¹⁵ The evolution of carbon dioxide from soils in the laboratory is effected by micro-organisms passing through the phase of decline (see page 62), and, during this period, the rate of gas evolution is not strictly proportional to the numbers of micro-organisms present. This being so, the plate count method can hardly be as efficient for estimating soil microbiological activity as a method depending on the measurement of the rate of formation of some product of metabolism, such as carbon dioxide. Nevertheless, carbon dioxide is not liberated as a result of the activities of *Nitrosomonas* and *Nitrobacter*, but neither are these organisms determined in the ordinary plate count.

The liberation of carbon dioxide from soil samples in the laboratory as a result of microbiological activity is expressed by the equation:

$$Y = Ftm,$$

where Y represents the total yield of carbon dioxide liberated in time t , and m and F are constants. Of these constants, m is a measure of the retardation in the rate of gas evolution due to laboratory conditions while F is the carbon dioxide evolved in the first time unit, that is, if t be the time in days, F is the yield of gas on the first day. This factor F has a practical significance.

In tropical Malaysia the soil temperature in the forest is constant and the mean daily temperature of soil in more open situations is sensibly constant. This being so it might be anticipated that, under normal circumstance, the numbers of soil micro-organisms and the microbiological activity of the soil would be constant. Such appears to be the case (see page 52), so that a knowledge of the amount of carbon dioxide liberated daily from the soil *in situ* will be of value, particularly for comparative purposes. This is where the factor F in the above equation is of practical importance, for the daily yield of gas from a soil sample in the laboratory on the first day must be very close to the actual value in the field. Usually it is not sufficient to measure the carbon dioxide evolved during the first 24 hours after sampling as a certain degree of irregularity is often evident during the short initial period, but if the measurements are continued until it is certain that the soil micro-flora have settled down, results are obtained which are reproducible within reasonable limits.

In Table IX are given some of the values of m and F obtained from soils in the Malay Peninsula.

TABLE IX
 m AND F VALUES OF SOILS FROM THE MALAY PENINSULA:
TEMPERATURE 26–29° C.

Origin of sample.	% Moisture.	m .	F .
Primary forest on the plains	11.7	0.55	19.1
Mangrove forest	36.2	0.85	6.5
Rubber plantation	32.8	0.63	13.1
Rubber plantation where a peat soil had been dressed with lime some three years previously	35.0	0.58	20.7

F represents the daily yield of carbon dioxide in milligrams per 100 grams of moisture-free soil at the beginning of the experiment.

It was found that the average value for F for the soils of the Malay Peninsula was in the neighbourhood of 15. Data obtained by Stoklasa¹⁶ showed the carbon dioxide (in milligrams) produced in 24 hours from 100 grams

of soil at 20° C. to be 1.0 for meadow soil, between 0.9 and 1.6 for a forest soil, and about 5.0 for fertile cultivated soils. From these figures it appears that carbon dioxide evolution in Malaysian soils is some ten times greater than in temperate regions during the summer months, and this in spite of the microbiological population being considerably smaller. It is possible that micro-organisms work more efficiently in equatorial regions in the absence of fluctuations in temperature but, in actual fact, the difference in total population is more apparent than real; in the humid tropics fungi predominate and play an important part in the decomposition of soil organic matter so that, although the soils under consideration contain fewer micro-organisms per gram than do soils in temperate regions, they contain a relatively greater weight of micro-organisms.

THE RELATION BETWEEN SOIL AND MALARIA

The nature of an aquatic flora or fauna is largely determined by the composition of the water, which, in turn, is conditioned by the underlying soil. In the sea and in large lakes the composition of the bed is relatively unimportant but, in ponds and puddles, the volume of water is small compared with the area of the underlying soil surface. It is hardly surprising, therefore, to find a relationship existing between the incidence of malaria and the nature of the soil. There appears to be no correlation between *pH* and malaria, and the effect of the geological formation beneath the soil is slight.

In the Malay Peninsula the incidence of malaria increases from the coast inland and reaches a maximum intensity at the foothills. The malaria-bearing anophelines prefer to breed in pure water, and Williamson¹⁷ has adduced evidence showing that the oxidation-reduction potential of a water has an important bearing on the presence of malaria. In water-logged soils, and in stagnant water containing decaying vegetable matter, conditions are unfavourable for malaria-bearing anopheline larvae and, in this connection, it is interesting to note that mangrove forests are by no means as malarial as might be anticipated.

It seems safe to conclude that the numbers of anophelines are reduced on sites where anaerobic biological processes are in operation. Shallow and stagnant pools do not find favour with malaria-bearing mosquitoes, and it has been shown that there is less malaria on the coastal peat soil of Malacca than further inland. Recent work by Williamson strongly suggests the possibility of reducing anophelines, especially the dangerous pure water species, by contamination of breeding places with organic debris.

SUMMARY

The most important plant constituents are cellulose, hemicelluloses, lignin and protein and the first two constitute about three-quarters of the total plant substances; much smaller amounts of simple carbohydrates, fats, waxes and mineral salts occur.

In the soil most of the plant remains are decomposed rapidly by micro-organisms, but lignin and protein combine to form a complex which is resistant to attack and so accumulates. Although, normally, proteins are readily decomposed by bacterial activity, when combined with lignin disruption by biological agency is very slow. Almost all the soil nitrogen is present in protein complexes.

Peat results when the decomposition of soil organic matter proceeds in the absence of adequate aeration (for example, under conditions of water-logging), and peat decomposition is effected largely by anaerobic species of micro-organisms.

Measurement of carbon dioxide evolution shows that microbiological activity in Malayan soils is some ten times greater than that in temperate regions during the summer months.

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SECONDARY GROWTH FOLLOWING DRASTIC CLEARING OF FOREST.

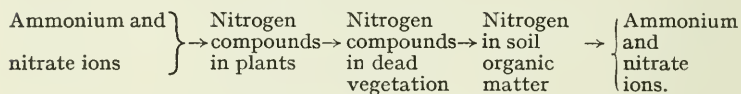
VII. THE NITROGEN CYCLE

OF the elements concerned in the biological changes which take place during the life of the growing plant, usually nitrogen is of most interest to the practical agriculturist, as it so frequently proves to be the limiting factor in crop production. Innumerable complex nitrogen compounds are present in the soil and in growing vegetation; as the plant ages new compounds are synthesized while others disappear, and small local variations in temperature, moisture content, etc., doubtless result in changes in the composition of the nitrogenous substances present in the soil. Change is an inevitable consequence of growth; in the ever-enduring forest there is little stability in the chemical composition of the vegetation, and the equilibrium existing in tropical forests is strictly dynamic and not static. It is instructive to consider the nitrogen transformations in some detail and to follow the essential changes occurring in so far as they affect the nitrogen atoms in circulation; in this cycle the air, growing plants, dead vegetation, the soil and the soil fauna all function as reservoirs of nitrogen.

THE NITROGEN CYCLE

The evidence available at present indicates that nitrogen can serve as plant nutrient material only when present in solution in the form of nitrates or, to a lesser extent, as ammonium salts. It appears that the intake of ammonium ions by plants is greatest in the early stages while nitrate absorption attains a maximum at the time of flowering, but both forms of nitrogen are taken up throughout the growth period.¹ The soil solution is absorbed by the root hairs of the plant, and in the leaves the nitrogen compounds are elaborated into highly complex organic substances, mainly protein in nature; the plant nitrogen thus remains immobilized until returned to the soil in the substance of seeds, dead leaves, etc. Dead vegetation is transformed

to soil humus by a series of changes effected through the agency of micro-organisms, and further microbiological activity results in disintegration of the humic material to ammonia, carbon dioxide and water. Oxidation of ammonia by biological or chemical means results in the formation of nitrate, which may be taken up by the growing plant, leached into the drainage water or, perhaps, under certain conditions, reduced to ammonia. The essential changes, therefore, in the nitrogen cycle are:



As a rule, the ammonium- and nitrate-nitrogen together comprise less than 1 *per cent.* of the total soil nitrogen but, although a considerable volume of research work has been carried out on the changes undergone by this "inorganic" nitrogen, precise information concerning the mechanism of some of the transformations is still lacking.

In temperate regions the proportions of nitrogen distributed between living vegetation, dead leaves, soil micro-organisms, etc., depend largely on the season, but in the primeval forests of Malaysia seasonal variation is inappreciable, the temperature is constant throughout the year, and it is safe to say that the proportions of nitrogen present in leaves, animals, micro-organisms and dead vegetation are constant and will remain so until disturbed by external forces. There are reasons for believing that, in the forests on the plains of Malaysia, the rate of decomposition of the soil organic matter is equal to the rate of formation so that, as a whole, the forest is neither losing nor gaining nitrogen. In soil in more open situations humus destruction outpaces its formation. In considering the nitrogen cycle in the equatorial tropics it is necessary to differentiate clearly between soil under forest and soil under secondary growth or crops. In the first case a condition of equilibrium is attained (Fig. 4), but in the second the soil may be losing or gaining nitrogen according to circumstances; a newly-cleared area will lose nitrogen (Fig. 5), but when such an

area is abandoned—in other words, when the surface is shaded and there is a return of dead vegetation to the soil—there is a slow reversion to the original condition, which

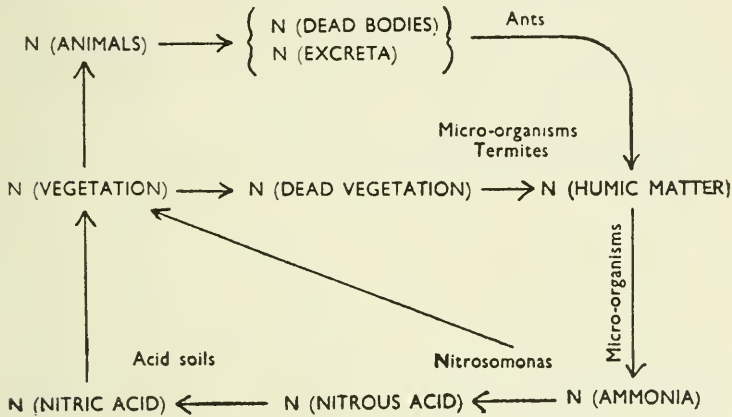


FIG. 4. THE NITROGEN CYCLE IN SOIL UNDER PRIMEVAL FOREST.

A condition of dynamic equilibrium is attained and any slight losses of nitrogen as nitrate in the drainage water are probably made up by the nitrogen compounds present in rain water.

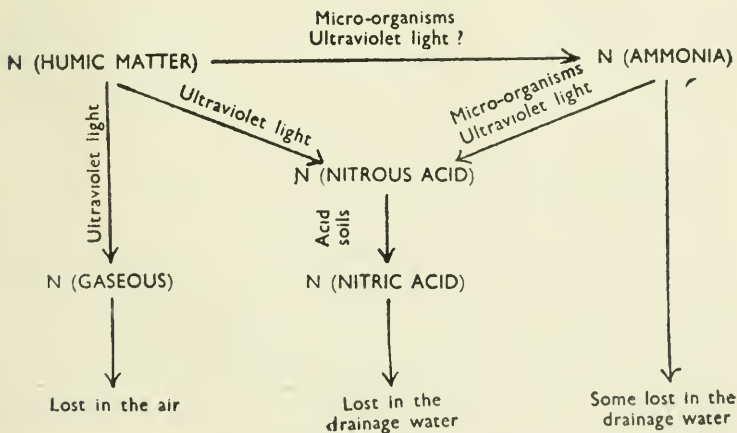


FIG. 5. THE NITROGEN CYCLE IN SOIL CLEARED OF FOREST AND EXPOSED TO THE SUN.

A continual loss of nitrogen occurs until a new and lower level is reached. The only slight additions are due to ammonia and nitric acid in rain water.

entails a very gradual accumulation of nitrogen (Fig. 6). The reason for these distinctions will be made clear in the next chapter.

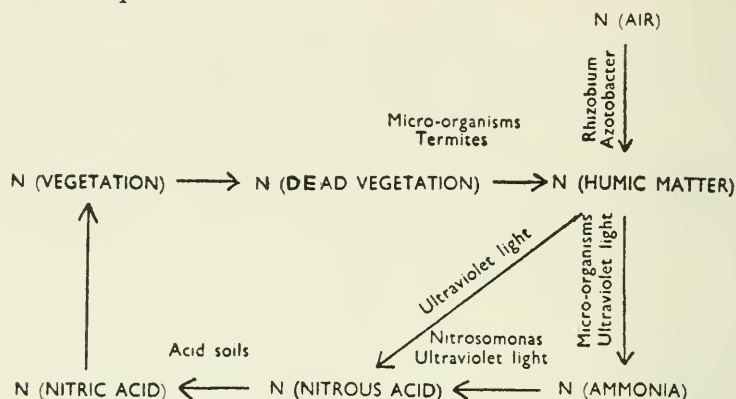


FIG. 6. THE NITROGEN CYCLE IN SOIL UNDER SECONDARY GROWTH.

Following clearing, increased shading results in a gradual replenishment of the nitrogen lost as a consequence of exposure of soil to the sun. The gain in nitrogen is due to the activities of nitrogen-fixing bacteria.

In view of the heavy rainfall in the humid tropics it is inevitable that a certain amount of nitrate should be lost as a consequence of drainage water finding its way into rivers, but it is improbable that, under the conditions of equilibrium in the forest, any losses are attributable to the evolution of gaseous nitrogen. To remedy the deficit, slight though it may be, there must be present some means of making additions of nitrogen to the system. It seems probable that rainfall is most important in this connection, for some 40 to 50 pounds per acre of nitric acid, and smaller quantities of ammonia, are returned to the soil by this means in the course of a year. It seems probable that nitrogen-fixing organisms, both symbiotic and non-symbiotic, are rare in forest soils; witness the scarcity of low-growing legumes in the shade of the Malaysian forests.

In the soil organic matter the C/N ratio is in the neighbourhood of 11, and it is evident that, if this ratio is to remain constant, some 11 parts of carbon must be oxidized

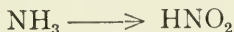
to carbon dioxide for every part of nitrogen converted to ammonia or nitrate during the process of decomposition. In the primeval forest a large proportion of the vegetation destined to become soil organic matter is in the form of timber, a material with a very high C/N ratio; in Malaysian soils the C/N ratio lies between 33 (peat) and about 9, so it is clear that much carbon must escape as carbon dioxide during the transformation of dead vegetation to soil humus.

INORGANIC NITROGEN COMPOUNDS IN THE SOIL

The best known transformations in the nitrogen cycle are those concerned with the formation of ammonia and nitric acid. When the pH value of a soil is above 7 the last-named compound is present as nitrate but, in the typical soils of Malaysia, the pH is always much below 7 so that acids rather than their salts persist.

It has long been known that ammonium salts are oxidized to nitrous acid and then to nitric acid by the agency of soil bacteria, and it was formerly thought that the process was entirely biological in nature; it has been shown recently that oxidation of ammonia in the soil may be effected by purely chemical means.^{2,3} Nitrification consists of two important stages:

(a) the oxidation of ammonia to nitrous acid,

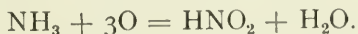


(b) the oxidation of nitrous acid to nitric acid,



(a) *The reaction Ammonia $\longrightarrow$ Nitrous acid.*

The conversion of ammonia to nitrous acid necessitates the presence of a sufficient supply of oxygen so that the reaction can proceed according to the equation:



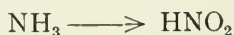
In soils in temperate regions this first stage in nitrification is effected largely, if not almost entirely, by *Nitrosomonas*, although it appears that a few other micro-organisms are

able to produce small amounts of nitrous acid from ammonium salts. *Nitrosomonas* is particularly sensitive to the reaction of the medium in which it works; but Gaarder and Hagem⁴ in Norway obtained weak nitrification by biological agency in media of *pH* below 2, and it may be that here, as well as in the acid soils of Malaysia, species or strains of *Nitrosomonas* occur which can tolerate acid conditions.

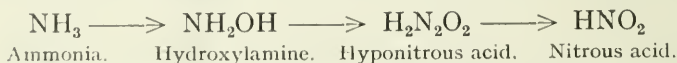
It has been established by Dhar and his co-workers that ammonia is converted to nitrous acid in the presence of sunlight and an adequate supply of oxygen and in the complete absence of micro-organisms; the writer has shown that nitrite formation can be effected in soils through exposure to ultraviolet light. There is a further type of chemical nitrification which is not yet clearly understood; it appears that nitrite formation can proceed in soil in the absence of micro-organisms and of light,⁵ and the writer has found that measurable amounts of nitrite can accumulate in soil subjected to a process of alternate wetting and drying-out.

There can now be little doubt that these chemical means of nitrite production are important, under certain conditions, in tropical soils. Although the evidence is incomplete, it is probable that the formation of nitrous acid in the soil proceeds by biological agency in the primeval forest while it may be effected largely by chemical means in soil on cleared areas exposed to the sun.

The expression

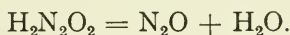


represents the final result of a series of reactions. It has been established by the writer that hydroxylamine and hyponitrous acid can occur as intermediate compounds during the oxidation of ammonia to nitrous acid, so that the complete cycle of changes may be shown as under:



As hydroxylamine is unstable at *pH* values above 5.0 and in the presence of nitrite, its existence in the soil can only be

ephemeral. On the other hand, hyponitrous acid, or its calcium salt, may occur in soil in measurable amount, but whether its presence is of any importance in the soils of equatorial regions remains to be investigated. Normally, hyponitrous acid escapes detection in soil during routine analysis, for on warming it decomposes to nitrous oxide gas and water



The information available at present indicates that, when the oxidation of ammonia to nitrous acid takes place, at usual temperatures and in neutral or slightly alkaline media, by biological or photochemical agency, there is no loss of nitrogen in any gaseous form, the whole reaction proceeding quantitatively.

(b) *The Reaction Nitrous Acid* $\longrightarrow$ *Nitric Acid.*

The oxidation of nitrous acid to nitric acid requires oxygen in accordance with the equation:



In the soil this oxidation can be effected by *Nitrobacter*, an organism which is sensitive to the reaction of the medium, although not so intolerant of acid conditions as *Nitrosomonas*. Until quite recently, it was supposed that this second stage in nitrification was always carried out by bacteria, but it has been demonstrated conclusively that nitrous acid is converted to nitric acid by chemical means in acid media. This nitrite loss may not be appreciable at *pH* values much above 5 but, under more acid conditions, the transformation is rapid. The relation between nitrite oxidation and the *pH* of the medium is shown in Fig. 7.³

In the presence of sunlight nitrates are reduced to nitrites, so that nitrite constitutes the final product when ammonium salts or nitrates are exposed to light; under acid conditions, of course, this nitrate reduction cannot become effective.

From the foregoing, it would appear that *Nitrobacter* can be responsible for the presence of nitrate only in soils whose *pH* number is well above 5, while in more acid media

the oxidation of nitrous acid is purely of a chemical nature. Many observers agree that *Nitrosomonas* is of more frequent occurrence in soils than is *Nitrobacter*. In the acid soils of Malaysia, it is probable that nitrification is effected by both biological and chemical agency. Under the shade of the primeval forest, nitrite formation in the soil may be

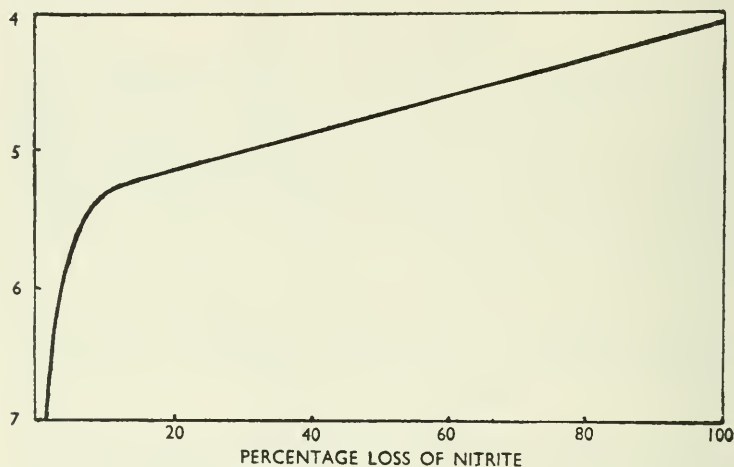


FIG. 7. THE TRANSFORMATION OF NITRITE TO NITRATE AT VARYING pH VALUES. (A. S. Corbet.)

The curve represents the amount of nitrite (0.22 gram potassium nitrite per 100 ml. solution) oxidized to nitrate at 32° C. in 8 days.

attributed to microbiological activity and the further oxidation to nitrate accounted for by the acidity of the medium. In cleared areas exposed to the tropical sun, *Nitrosomonas* or some allied organism may be responsible for the appearance of nitrous acid but, at least at the soil surface, this compound can result from the operation of chemical processes. As in forest soils, the pH value on cleared soils is usually sufficiently low to ensure immediate oxidation of nitrous acid to nitric acid.

Doubt has been expressed as to whether nitrification is as important in forest as in cultivated soils: it is well known that, in temperate regions, fungi are relatively more abundant than bacteria in forest soils, and many species of the former are associated with production of ammonia.

Aaltonen considered that, unlike other plants and shrubs, forest trees may not receive nitrogen in the form of nitrate.⁶ In this connection it is interesting to note that ammonium sulphate has usually a more stimulating effect on the growth of *Hevea brasiliensis* than has nitrate.

Although the photochemical reduction of nitrate to nitrite takes place quantitatively, the biological process of denitrification results in the loss of nitrogen in a gaseous form. It does not appear probable that denitrification processes are responsible for any serious losses of nitrogen from the soils of Malaysia, except under conditions of water-logging for, excepting swamp and peat soils, anaerobic micro-organisms are scarce in Malaysian soils and denitrification is an anaerobic process.

LOSSES AND GAINS OF NITROGEN

It has already been pointed out that, in the rain forests of Malaysia, gains or losses of nitrogen in the soil must be inappreciable compared with the total quantity of this element which is involved. And, moreover, any losses of nitrogen which occur as a result of nitrates finding their way into the drainage water and thence into streams and rivers are probably balanced by nitrogen returned to the system in rain water.

The case is very different with soils exposed to the action of the elements, however, for here raising or lowering of the nitrogen content of the soil will take place according to circumstances.

Additions of nitrogen to the soil are the result of activities of both symbiotic and free-living micro-organisms. The rôle played by nodule bacteria found on the roots of legumes has been mentioned already (page 49), but other nitrogen-fixing bacteria occur on the leaves of certain plants and on the roots of some non-leguminous plants. Shrubs and low-growing plants pertaining to the family Leguminosae are rare in the Malaysian forests, and it appears probable that they play a minor part in the nitrogen cycle under such circumstances. In the tropics in general, leguminous plants are found in sunny situations, and it is here that their

offices in fixing atmospheric nitrogen are needed most, for nitrogen losses are considerable when the soil loses the shade offered by forest trees.

Of the two important groups of non-symbiotic nitrogen-fixing bacteria, of which *Azotobacter* and *Clostridium* may be taken as representative examples, the first-named is sensitive to acid conditions and occurs more frequently in cultivated than in virgin soils. It has been stated that the *pH* limit for the occurrence of *Azotobacter* is 6.0, yet the presence of this organism has been demonstrated in many Javanese and Indian soils.⁷ Altson has isolated *Azotobacter* from typical Malayan soils and has shown that isolations were able to fix nitrogen in culture.⁸ Of the anaerobic nitrogen-fixing organisms, *Clostridium butyricum* Prazm. (= *C. pastorianum* Win.) is the best known; the optimum temperature for its development is between 28° and 30° C., and, although the optimum *pH* is almost at the neutral point, this organism has been found in soils as acid as *pH* 5.0. Practically nothing is known regarding the occurrence of *Clostridium* in Malaysian soils.

The fact that *Azotobacter* and *Rhizobium* are more resistant to ultraviolet light than most species of bacteria is probably not without significance, as these organisms are more active in exposed soils than under the dense shade of primeval forest.^{9,10}

It is generally conceded that the nitrogen losses which take place in soils recently cleared of cover and exposed to the sun may be very considerable. Those interested in gardening in Malaysia are only too well aware of the necessity of constantly replenishing the supplies of organic matter in the soil. From work carried out by the writer, it appears that the nitrogen escapes from the soil mainly as nitrogen gas and that comparatively small amounts are lost as ammonia and nitrate.¹¹ That such losses of gaseous nitrogen are serious there can be no question, and the theoretical and practical aspects of the matter are discussed in the following chapters.

The nitrogen status of the soil appears to be related, not only to the mean annual temperature and humidity, but



MIMOSA PUDICA, THE SENSITIVE PLANT, ALWAYS TO BE FOUND GROWING IN PROFUSION IN OPEN SPACES IN MALAYSIA.

also to the amount of solar radiation received and, when equilibrium is attained, cultivated and exposed soils in Malaysia have a lower nitrogen content than those of the well-shaded forest. However, under natural conditions in soils exposed to the glare of the sun, it is not long before the soil temperature and insolation are reduced and the surface shading increased as a result of the growth of vegetation—be it only lalang—and both symbiotic and non-symbiotic nitrogen-fixing bacteria come into operation. In Malaysia, leguminous plants are always to be found in open sunny situations, although it must be emphasized that not all species of the family harbour the *Rhizobium* nodule-forming bacteria on their root systems. Nodules are present in the subfamily Mimosaceae, but all the Caesalpinaceae examined by various investigators have been found to lack nodules.¹² It has been suggested that the absence of nodules on various leguminous plants does not necessarily preclude the presence of nitrogen-fixing bacteria within the root tissues but, during a careful investigation of *Cassia tora* in the Hawaiian Islands, micro-organisms were not found in any of the tissues examined.¹³ In Malaysia, the sensitive plant (*Mimosa pudica*) always appears at roadsides and in neglected corners of gardens, and it is known that this plant harbours nodule-forming bacteria. Many of the leguminous plants employed as covers on rubber plantations, such as *Crotalaria anagyroides*, *Dolichos hosei*, *Centrosema pubescens*, and *C. plumieri*, have been examined by the writer and found to possess nodules on the root systems.

From the foregoing it might be thought that the process of restoring to the soil the nitrogen lost by wrong and extravagant methods of clearing and cultivation might be left to nature: this may be true; but the process takes many decades and there is no doubt that the most economical procedure is to conserve the nitrogen already in the soil as far as possible, rather than to look round for methods of making good the depletions.

The nitrogen cycle in soil under secondary growth following clearing is shown diagrammatically in Fig. 6. In Fig. 5

is shown the probable course of the nitrogen cycle when soil cleared of forest is exposed to sun and rain in the absence of cover. To summarize, it may be said that, except for ammonia and nitric acid in the rain water, any increase in soil nitrogen depends on biological activity, while, under usual circumstances in Malaysia, losses appear to be due mainly, if not entirely, to physico-chemical processes.

THE RECOLONIZATION OF KRAKATAU

At this point it is interesting to consider the recolonization of the Krakatau Islands in the Sunda Strait. It seems most improbable that any forms of life survived the terrific eruptions which occurred in August, 1883, and left the islands covered with a layer of hot ashes and pumice to a depth of 30 to 60 metres.¹⁴ At the present time, the islands are clothed with forest and have quite a considerable flora and fauna; nevertheless, the inland forest is not the primary forest association of the lowlands of Malaysia, but appears to have rather the character of an advanced secondary association.

It might be supposed that nitrogen-fixing micro-organisms were the pioneers in the recolonization of Krakatau, but it seems more probable that the nitrogen reaching the islands in the rainfall is sufficient for the requirements of small, stray, wind-borne organisms which could easily maintain a footing when once established. With an annual rainfall of 100 inches, the nitrogen deposited as nitric acid and ammonia in this part of the world is of the order of 24 pounds per acre per annum.¹⁵

The plant associations on Krakatau have been those which would have occurred on the larger islands of Malaysia during the reversion of cleared land to forest. Earlier observers reported the presence of large tracts of lalang (*Imperata arundinacea*) and elephant grass (*Saccharum spontaneum*) and, later, there appeared the common plants of secondary associations, such as *Melastoma malabathricum*, stag-horn moss (*Lycopodium cernuum*), the fern *Blechnum orientale*, *Casuarina equisetifolia* and *Lantana*

camara. It is of particular interest that Ernst reported in 1906 that, both on the strand and in the inland zone, the number of individual plants pertaining to the Leguminosae almost equalled that of all the arborescent and shrubby plants belonging to other families.¹⁶

In 1928, the numbers of terrestrial plant and animal species recorded from the Krakatau Islands were 276 and 751 respectively.

SUMMARY

The nitrogenous material in the soil is decomposed by biological agency to ammonia and nitric acid and these compounds are absorbed by the root systems of growing vegetation.

It appears that a state of dynamic equilibrium exists in the primeval forests of Malaysia and the slight nitrogen losses due to leaching of nitrate are balanced by ammonia and nitric acid returned to the system in the rain water.

In cleared areas exposed to the sun, nitrogen disappears rapidly from the soil until a new and lower level is reached ; with the subsequent appearance of a vegetative cover, and consequent shading of the soil, there is a gradual increase in the nitrogen content of the soil as a result of the activities of symbiotic and free-living nitrogen-fixing bacteria.

The nitrogen losses from tropical soils exposed to the sun appear to be effected by a chemical mechanism, entailing release of nitrogen gas, with smaller losses of ammonium salts and nitrates in the drainage water. Whether a soil is gaining or losing nitrogen depends largely on the amount of solar radiation received.

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VIII. JENNY'S LAW

Although it has long been known that the distribution of organic matter in the soil is closely related to climatic conditions, it is only within the last few years that the subject has been approached from the mathematical standpoint. Jenny¹ first showed the nitrogen and organic matter content of the soil to be functions of the temperature and humidity, and as his conclusions are of vital importance to tropical agriculture, they are considered here in some detail.

According to Jenny, when climate is considered in relation to soil conditions it is found to consist of three primary factors, temperature, precipitation and evaporation, but the ratio of the last two may be expressed as the *humidity factor*. The nitrogen content of the soil is a function of the mean annual temperature and the humidity, or expressed mathematically:

$$N = f(t.H),$$

where N is the nitrogen content of the soil, t the mean annual temperature and H the humidity factor

$$\left(\text{i.e.} = \frac{\text{precipitation}}{\text{evaporation}} \right).$$

There are many regions on the earth's surface where the ratio precipitation/evaporation is constant: this condition obtains practically throughout Malaysia and Jenny based his calculations on belts of constant humidity in the United States of America. When the humidity factor is constant the equation becomes

$$N_H = f(t),$$

but this gives no information concerning the precise nature of the relationship. Biological processes are commonly represented by sigmoid curves and it would be anticipated that the relation between the nitrogen content of the soil and the mean annual temperature would be represented by such a curve. Jenny has shown that, for soils in North

America in the same humidity belts, the relation between the soil nitrogen and the mean annual temperature is exponential and can be expressed by the equation:

$$N_H = \frac{a}{(1 + e^{kt})},$$

where N_H and t have the same significance as before, e is the base of natural logarithms and equal to 2.718, and a and k are constants. This equation is regarded as a first approximation of a fundamental law and it is stated that the nitrogen content of the soil decreases exponentially with increasing temperature, provided that the same humidity factors are operative.

The same equation expresses the relation between the organic matter (or carbon²) content of the soil and the temperature, but the numerical values of the constants a and k are different for the C/N ratio decreases with increasing temperature. Jenny has shown that this ratio decreases from 15 to 9 in passing from north to south in North America: in Malaysian soils this ratio appears to be higher than would be anticipated from these considerations, but it may well be that this anomaly is more apparent than real.

Jenny has shown that the nitrogen content of the soil increases with increasing humidity, if the temperature is maintained constant, but in tropical and subtropical soils the high temperature keeps the soil nitrogen at so low a level that moisture conditions are of very secondary importance. It is evident that the law governing the nitrogen-temperature relationship and the variation in the C/N ratio discussed above can be operative only within certain limits, for microbiological activity is inhibited both at low and at high temperatures, and beyond a certain temperature range the equation given on this page cannot apply. With low temperatures, when microbiological activity in the soil is slight, the C/N ratio approaches that of the overlying vegetation.

The enunciation by Jenny of these laws relating soil organic matter with the mean annual temperature and humidity marks a very great advance in soil science, but

there appears to be no doubt that a further factor, that of insolation, is important in determining the nitrogen status of any given soil. In general, there is parallelism between the mean annual temperature and the solar radiation received per annum and so the effects of sunlight are often obscured; nevertheless, high temperature unaccompanied by exposure to strong sunlight is of itself insufficient to produce the effects predicted by Jenny's law. In so far as these considerations apply to Malaysia, it appears that Jenny's theorem should be re-stated as follows: THE NITROGEN AND ORGANIC MATTER CONTENT OF THE SOIL DECREASE WITH INCREASING INSOLATION AND TEMPERATURE, PROVIDED THAT THE SAME CONDITIONS OF HUMIDITY OBTAIN.

THE RELATION BETWEEN TEMPERATURE AND HUMUS FORMATION AND DECOMPOSITION

The optimum temperature for humus accumulation differs from that for humus decomposition so that, in presence of an adequate supply of moisture and air, the extent to which organic matter accumulates in the soil depends on the mean annual temperature.³ Humus formation is favoured by a luxuriant growth of vegetation and, in turn, a rich macro-flora is promoted by strong sunlight (which ensures vigorous assimilation), a fairly high temperature and a sufficiency of moisture. Thus humic formation may be taken as corresponding to the curve *A* in Fig. 8 which represents the relation between vegetative growth and temperature; plant growth is inhibited both at low and at high temperatures and has an optimum in the neighbourhood of 20°–25° C.

Humus decomposition is effected largely by the soil micro-organisms, whose activities are favoured by high temperature and adequate moisture supplies but are not directly dependent on solar radiation. The soil micro-flora cannot withstand extreme temperatures and have an optimum between 30° and 35° C. The relation between humus decay and temperature is depicted by curve *B* in the figure. The graphs for humus formation and humus decomposition

intersect at about 25°C . as at this temperature the two processes proceed at the same speed and there is no accumulation of organic matter in the soil. At temperatures below $20^{\circ}\text{--}25^{\circ}\text{C}$. humus formation outpaces its decay and at temperatures above 25°C . the reverse is the case: these

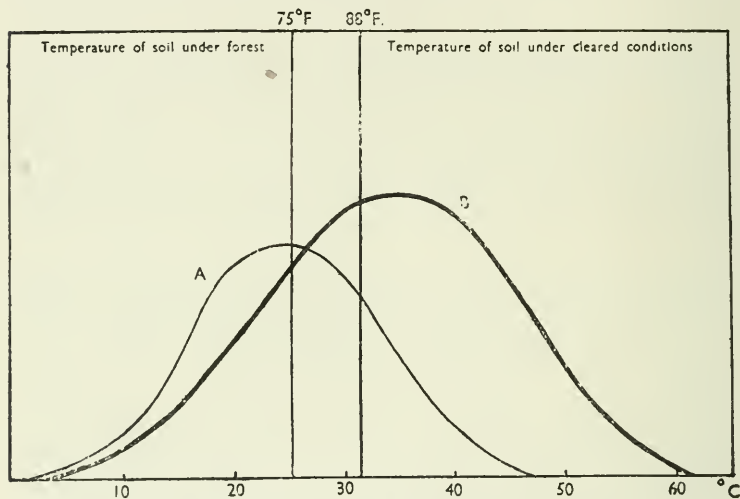


FIG. 8. THE RELATION BETWEEN TEMPERATURE AND HUMUS FORMATION AND DECOMPOSITION. (Adapted from E. C. J. Mohr.)

The graph (A) represents the growth of vegetation, showing that, in general, plant growth ranges from 5° to 45°C ., with an optimum at $20^{\circ}\text{--}25^{\circ}\text{C}$. This curve also portrays the conditions under which humus formation can take place. The curve (B) shows the relation between microbiological activity and temperature, the range being from 5° to about 60°C ., with an optimum between 30° and 35°C . Humus decomposition depends on the activities of soil micro-organisms and so curve (B) expresses the conditions under which this process can take place.

It is evident that humus accumulation can take place only at temperatures below 25°C . At 25°C . humus formation and decay proceed at the same rate and so the organic matter content of the soil remains constant.

temperatures are in the nature of approximations but they may be taken as correct for all practical purposes. The important fact emerges that THERE CAN BE NO ACCUMULATION OF ORGANIC MATTER IN THE SOIL AT TEMPERATURES ABOVE 25°C . This generalization, however, does not apply to water-logged and peat soils where anaerobic conditions obtain.

THE NITROGEN CONTENT OF MALAYSIAN SOILS

Application of the principles discussed in this chapter to the soils of Malaysia yields results of considerable importance to the practical agriculturalist. The humidity factor may be regarded as constant so that, in Malaysia, the nitrogen and organic matter content of the soil are related to the insolation and the temperature. In the forests on the plains of the Malay Peninsula the soil temperature at or near the surface is slightly below $25^{\circ}\text{C}.$, the daily variation being less than 1° , and these results may be taken as being of general application throughout Malaysia: in such soils the rates of humus formation and decomposition are equal so that there is neither loss nor gain of humus.⁴ As the hills are ascended the temperature falls and it would be expected that the organic matter content of the soil would increase. Observation shows that this is actually the case, but the precise relationship between the nitrogen content of the soil and altitude has not yet been studied in Malaysia. It has been stated that, in general, a fall of $10^{\circ}\text{C}.$ in the mean annual temperature results in increasing the average nitrogen content of the soil some two- or three-fold. The relation between elevation and nitrogen content of the soil in Colorado has been examined by Hockensmith and Tucker and their results show that, at altitudes between 5000 and 10,500 feet, an exponential relationship exists, as would be deduced from Jenny's law.⁵ It is probable that the C/N ratio is slightly higher on the forested hills of Malaysia than on the plains for, at high altitudes, conditions tend to approach those which obtain in temperate regions.

On the plains, where the high temperature militates against the accumulation of humus, the organic matter content of the soil is low, and to quote Rahmann, "Tropical forest works with a small capital of nutrients and a rapid turnover." When the dense primeval forest is envisaged, it seems remarkable that the soil can be so poor in organic material; yet it is not uncommon to find patches of jungle

soil entirely devoid of humus. Where there *is* any considerable layer of humus the explanation is to be sought in the presence, now or formerly, of factors inhibiting aerobic decomposition. In the forest extensive areas of marsh-land are encountered and often local conditions obtain which result in small areas being more or less permanently water-logged, and it is here that decomposition proceeds by slow anaerobic processes. Several observers have drawn attention to the occasional occurrence of quantities of humic matter under lalang, but there is no reason for supposing that the explanation of this apparent anomaly is other than that given above, for the presence of this weed usually indicates recent clearing and, therefore, the possibility of a water-logged site having been drained.

The forested plains of Malaysia are of particular interest to the soil microbiologist for the soil temperature is constant, and this temperature is that at which humus formation and decomposition proceed at the same speed. As the hills are ascended the mean annual temperature decreases and humus accumulation becomes possible. It is apparent that there is some mechanism in operation maintaining the soil nitrogen and carbon at a definite level according to the soil temperature and amount of insolation received, and it is now possible to envisage clearly the consequences of felling jungle and exposing the soil to the sun during clearing operations. Such a procedure has immediate and important results: the temperature is raised and the soil is exposed to the direct action of the sun and, for the time being, there is a complete cessation of any addition of organic material to the soil system.

When clearing takes place on the plains, as it usually does, before equilibrium can be attained the organic matter content of the exposed soil must fall to a new level in accordance with the considerations advanced above. That is to say, the increase in insolation and temperature, consequent upon felling and clearing, is followed by a loss of humic matter and such losses continue until the level for the new set of conditions is reached. It is evident that, under such circumstances, addition of nitrogen to the soil can have only



CLEARING FOREST FOR RUBBER CULTIVATION.

a transient effect; in fact, in the absence of growing vegetation such nitrogen can neither be utilized by the plant nor retained by the soil particles but is speedily lost.

LOSSES OF NITROGEN FROM CLEARED AREAS

It is now being realized that the loss of nitrogen which follows increased soil temperature and exposure to the sun may be very considerable, and Wilshaw has suggested that, under such conditions, decomposition of soil organic matter proceeds at a far greater rate than is generally supposed.⁶ Recently, this investigator has shown that, in soil exposed in pots in Malaya, the total nitrogen content (as determined by the Kjeldahl method) dropped from 0.170 to 0.105 *per cent.* in seventeen weeks.⁷

The precise manner in which any nitrogen present in excess over that which can be retained under given conditions of insolation and temperature escapes from the soil is a matter of paramount importance. In this connection it must be remembered that the soil systems on most rubber estates are not in a state of equilibrium: such is certainly not the case with the older clean-weeded plantations where almost all soil organic matter has long since vanished, but the reason for this is considered on page 105. In the past it has been generally assumed that any increase in soil temperature results in a speeding up of the microbiological processes whereby the humus is rapidly oxidized to carbon dioxide, nitrate and water, but it is now known that this explanation is not correct, for the writer has shown that no significant changes occur in the soil microbiological population as a result of forest clearing.⁸ Humus decomposition is effected by aerobic species of fungi and bacteria which normally appear on agar plates, and there can be no reason for supposing that the opening-up of forest (with consequent increase of soil temperature and exposure of the soil surface to the sun) results in the appearance of large numbers of micro-organisms able to decompose soil organic matter but incapable of growing on ordinary culture media.

If this organic matter disappearance is not biological in

nature it must be a physical or chemical process, but the most important physical factor is erosion and it is known that the amount of organic material lost from the soil by such mechanical means does not nearly account for all the losses. It becomes evident then that the mechanism responsible for the losses is chemical in nature: mere exposure of soil to high temperature in a humid atmosphere does not result in conversion of humic material to a soluble form which may be lost in the drainage water, nor does an alternating process of drying and washing-out, such as occurs almost daily in newly-cleared areas in equatorial regions, effect any appreciable transformation of soil organic matter into soluble form. Almost the only possibility left is that increased insolation is responsible for a photochemical change which results in humic matter being broken down to carbon dioxide and nitrogen, together with smaller quantities of ammonia and nitrate, and experimental evidence has been adduced which shows that this explanation is almost certainly the correct one.⁹ Wilshaw opined that nitrogen was probably lost from the soil in gaseous form but he attributed the losses to increased bacterial activity. The precise nature of this chemical mechanism, which results in losses of nitrogen from exposed soils, is obscure but it has been shown by the writer in the laboratory that such nitrogen losses occur rapidly when soil is exposed to ultraviolet light in the presence of free alumina. Under the experimental conditions described, the fall in the nitrogen level is not continuous but ceases when a certain value has been reached, which is in accord with the views developed earlier in this chapter. The results obtained by Hardy show that free alumina is present in quantity in the lateritic soils of the equatorial tropics.¹⁰ It is possible that the release of elementary nitrogen from the soil, under the tropical conditions considered, is in some way connected with the formation of hydrogen peroxide by the the action of ultraviolet light. Nevertheless, the difficulty in accepting this as a complete explanation of the phenomenon is the apparent failure of ultraviolet light to penetrate any distance below the surface of the soil.

It is apparent from the foregoing that, in the absence of shading, it is not possible to increase the nitrogen content of soils on the plains of Malaysia beyond a certain low level, which is below that normally found in soils under forest. In the surface soils of the sugar cane districts in Java, for instance, the average amount of nitrogen present is 0.076 *per cent.*¹¹ Addition of nitrogenous matter, whether in the form of inorganic fertilizers or as green manure, cannot result in a permanent increase in the nitrogen status of the soil, and such additions can be justified only in the presence of growing vegetation ready to assimilate immediately the products of decomposition. Even so, a large proportion of the nitrogen in added manure may disappear into the air in the form of elementary nitrogen.

When a cleared area is left to recuperate there is, usually, an immediate growth of lalang grass, followed subsequently by the appearance of other weeds and shrubs; in this manner the soil temperature and the amount of solar radiation received are lowered, so that it is possible for the soil gradually to retain slightly increasing amounts of nitrogen. In areas under secondary associations, almost invariably there is a good growth of species of Leguminosae known to bear root nodules as a consequence of the presence of nitrogen-fixing bacteria, and it appears also that certain non-symbiotic organisms, such as *Azotobacter*, are partly responsible for the return of nitrogen to the soil when temperature and shade conditions permit of restoration to a higher level. In Fig. 9 is given a diagrammatic representation of the course of the nitrogen changes in the soil when primary forest is cleared, and then subsequently allowed to revert to jungle.

On old plantations, which have suffered severely from the application of clean-weeding principles, it is improbable that the nitrogen content of the soil is as high as it should be under the conditions of shading and lowered temperature which normally obtain. The reason for this is not far to seek—although the loss of nitrogen and organic matter consequent upon exposure of soil to the sun is a chemical reaction, the reverse process is biological in nature, and

humus formation and nitrogen fixation cannot take place in an absolutely sterile soil.

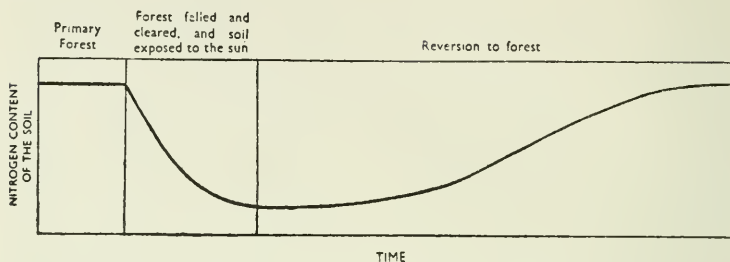


FIG. 9. A DIAGRAMMATIC REPRESENTATION OF THE CHANGES IN THE NITROGEN CONTENT OF THE SOIL WHEN PRIMARY FOREST IS CLEARED AND THEN SUBSEQUENTLY ALLOWED TO REVERT TO JUNGLE.

Under primary forest the nitrogen content of the soil is constant. When the forest is felled and cleared and the soil is exposed to the sun there is a rapid loss of nitrogen (mainly in the gaseous form). When cleared land is abandoned the degree of soil shading is gradually increased with succeeding secondary plant associations and the nitrogen content of the soil slowly returns to its normal value for forest soil.

SUMMARY

According to Jenny, the nitrogen (and organic matter) content of the soil varies inversely with the mean annual temperature and directly with the humidity but it is now evident that, in Malaysia, the nitrogen content of the soil decreases with the amount of solar radiation received.

It has been shown also that at temperatures above 25°C . humus decomposition outpaces its formation but at temperatures below 25°C . there is a gradual accumulation of soil organic matter.

The soil temperature in the Malaysian forests is 25° , so that the nitrogen content remains constant. When the insolation is increased by felling and clearing forest, the nitrogen content of the soil drops to a new and lower level and can only be permanently increased above this value in the presence of adequate shading.

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2. The soil organic matter = organic carbon $\times$ 1.74.
3. E. C. J. Mohr, *De Grond van Java en Sumatra*, 2nd ed. (Amsterdam), 1930.
4. Actually, the balance is slightly in favour of humus formation.
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IX. SOME PRACTICAL CONSIDERATIONS

THE BURNING OF CLEARED LAND

SOME controversy has centred around the question as to whether timber and other forest debris on newly-cleared land should be burned or allowed to decay on or near the site. In parts of tropical Africa, this burning of forest waste on cleared land prior to cultivation is practised as a religious rite. In tropical Asia, and particularly in the Malay Peninsula, the custom of burning timber and dead vegetation on land cleared for agricultural purposes is followed almost invariably, but there is no reason for supposing that the practice is the outcome of detailed consideration of all the factors involved. Among the more enlightened sections of planting communities, "burning-off" is advocated primarily on account of the fear that decaying timber may be a reservoir for pathogenic fungi, later to prove troublesome to the crop; but to some extent also as a result of a desire to have plantations neat and orderly. At first sight the process strikes one as being a squandering of natural resources, but local conditions are such that removal of timber from the site of clearing is not an economic possibility. It is not generally appreciated that very few of the trees of a tropical rain forest produce timber of commercial value, so that the issue is really concerned with burning the timber after felling or permitting it to decay *in situ*. The practice of burning cleared land has been vigorously defended by Milne who has advanced the following points in favour of this procedure¹:—

(a) The mineral constituents of the forest debris are retained on the site.

(b) Addition of a large quantity of organic matter of high C/N status is undesirable as its decomposition will entail the immobilization of, perhaps, the whole of the available nitrogen of the soil.

(c) The destruction of the soil humic matter under the usual conditions of burning is inappreciable.

(d) Reduction in the numbers of soil organisms as a consequence of burning may have the beneficial effects of a partial sterilization.

(e) Although there will be some permanent loss of sulphur and phosphorus in the volatile products of combustion, the nitrogen loss due to a similar cause may be very slight on the balances of all the processes involved.

(f) The ground is cleared of trash which would support a dubious population of fungi and termites and, perhaps, encourage fires.

In discussing the subject the fate of the mineral salts and soil organic matter will be considered before dealing with the question of danger from pests and diseases.

THE EFFECT OF BURNING ON THE SOIL MINERAL SALTS

Pitcaithly and Worley have drawn attention to the important rôle played by large, deep-rooted, forest trees in New Zealand in bringing to the surface mineral matter essential to plant growth.² Destruction of the trees places the source of the supply of minerals out of reach so that the existing stock has to be conserved or the depletions have to be made good by the application of fertilizers.

If vegetable waste is allowed to remain and decay on the site of clearing, mineral constituents are gradually returned to the soil under conditions whereby they stand every chance of being assimilated by a growing crop or cover. When vegetation is reduced to ashes by burning there is an immediate increase in the *pH* value of the soil, and a very temporary increase in the population of soil micro-organisms as a consequence of the presence of wood ash. In the absence of growing vegetation, the potassium present in the wood ashes³ is adsorbed by the soil colloids and it is improbable that any appreciable losses of metal ions occur as a result of base exchange; under the usual circumstances, losses of mineral plant nutrients by leaching must be slight.

Destruction of the plant debris by burning renders the mineral constituents immediately available, and whether this is desirable or otherwise depends, to a large extent, on the crop following. In any case, depletions in the stock of mineral salts by a succession of annual crops will ultimately necessitate the application of fertilizers.

BURNING AND THE SOIL ORGANIC MATTER

The dead vegetation left after felling consists largely of stems, branches and tree trunks, all of which have a high C/N ratio. Figures recently published show the C/N ratio for certain typical low-growing Malayan plants to range between 21 and 10 for the leaves and between 58 and 14 for the stems,⁴ but the ratio for timber is not less than 200. It is well known that decay of organic matter of low nitrogen status, by microbiological agency, results in the immobilization of a certain amount of the nitrogen present in the soil, for the growth and multiplication of micro-organisms demands a supply of nutrients in which the C/N ratio is approximately 10 for fungi and 5 for bacteria. If micro-organisms effected the decomposition of timber it would certainly be necessary for them to remove nitrogen from the soil to make good the deficiency of this element in the material being disrupted. With perennial crops, however, this aspect of the question is far from being a disadvantage; in fact, it may be considered as a reason for allowing the timber to decay on the site, for this temporary immobilization of soil nitrogen on recently cleared land is desirable, particularly when a permanent crop, such as rubber, is to be established. It has been pointed out already (page 99) that exposure of the soil to the sun results in a diminution in the total nitrogen content, and this loss will be accentuated when no replenishment of organic matter takes place for some years. Under such circumstances, the position is that the soil is not only "living on capital" as it were, but is doing so at an increased rate of expenditure. It has been shown that the process of burning is responsible for a greatly increased bacterial population at or near the site of firing, but, although this increase is very ephemeral, it



NEWLY-PLANTED RUBBER SEEDLINGS. NOTE HOW THE SOIL WHICH HAS BEEN RECENTLY CLEARED
OF FOREST IS EXPOSED TO THE SUN.

must account for the breakdown of a small amount of humic matter. In the absence of vegetation the nitrates elaborated as a consequence of biological and chemical activity will not remain long in the soil but will disappear in the drainage water.

It seems clear that a process whereby nitrogen is retained in the soil during an initial period, when heavy losses are inevitable, and is gradually returned to the soil at some later date, when the available supplies of this element have been depleted, is of considerable economic value when dealing with a perennial crop and the alleged disadvantages of the "natural decay" method should be investigated very completely before the practice is condemned as unworkable.

In actual fact, however, it appears that micro-organisms play a very insignificant part in the decompositions of timber in equatorial regions, such decay being accomplished very largely, if not entirely, by termites. It is believed that these insects obtain nitrogen supplies through the agency of nitrogen-fixing intestinal protozoa and, if this is so, decaying timber must be placed on the credit and not on the debit side when drawing up a nitrogen balance sheet.⁵

THE EFFECT OF BURNING ON THE SOIL MICRO-FLORA

It has been stated on page 103 that the generally accepted view that increased temperature, consequent on clearing forest, results in a speeding-up of the microbiological processes responsible for decomposition of soil organic matter can no longer be upheld. Forest clearing in Malaysia is without effect on the numbers of soil micro-organisms, as determined by the plate count method.

The effects of the heat generated by burning brushwood are very localized, and as Milne observes, the destruction of humic matter under a running fire is inappreciable. The actual burning operations are also without effect on the soil micro-flora, but addition of wood ash to the soil is reflected in a greatly increased microbiological population though this phenomenon is strictly localized and of short duration. Under no circumstances is there a reduction in the numbers of soil micro-organisms.

PESTS AND DISEASES HARBOURED BY DECAYING TIMBER

From the economic standpoint, the question of danger to a growing crop from pests and diseases harboured by timber and plant debris left to decay *in situ* is a matter of prime importance. Loss as a result of infection by pathogenic fungi will, in general, be much more serious than damage inflicted by termites.

Dr. J. R. Weir, of the Rubber Research Institute of Malaya, arranged a series of experiments at the Institute's Experiment Station in which direct comparison of the incidence of root disease on *Hevea brasiliensis* under cleared and uncleared conditions was possible. These experiments were in progress for rather more than three years before the results were analysed by Napper,⁶ who was concerned mainly with the presence of *Fomes lignosus*, one of the two most destructive root diseases of the rubber tree in Malaysia and often responsible for heavy losses during the first five years in the life of a plantation.

It has been tacitly assumed that the incidence of root disease in a planted area varies directly with the total amount of timber remaining in the soil at the time of planting, and so the larger the proportion of the timber removed at this time, the lower will be the subsequent losses due to root disease. The acceptance of this principle entailed the burning-off of dead vegetation, followed by removal of the remaining debris as far as possible. It was considered uneconomic to unearth the last remnants of buried timber as these could hardly be responsible for any considerable incidence of disease.

The results obtained by Napper appear to show that, up to the age of three years, rubber trees are exposed to a greater risk of infection from *Fomes lignosus* in an area from which surface timber and jungle stumps *have been removed* than in an uncleared area. It was found also that the amount of disease was less under a cover than on a clean-weeded area and still less where secondary forest growth was

established as a cover. Although the published results appear to be definite, it is too early to conclude that infection by pathogenic fungi is invariably less in uncleared than in cleared sites at all ages in the life of a plantation: nevertheless, it seems probable that further work along these lines may show that "burning-off" and "clean-clearing" are practices which have little to commend them on economic grounds.

Napper supposes that *Fomes lignosus* is present in the jungle stand before clearing, and that *complete* removal of all the timber before planting would eliminate entirely any danger of infection. Such a counsel of perfection, however, is quite beyond the bounds of practical politics and a certain amount of timber must always be left in the soil. Under the usual conditions of clean-clearing, the food material available for the fungus is small and soon exhausted; this results in the formation of rhizomorphs which wander through the soil until they encounter further food material which—under the usual planting conditions in Malaysia—will be the roots of a rubber tree. The presence of a woody plant, such as *Crotalaria*, known to be susceptible to attack from *Fomes*, tends to reduce the incidence of disease on the rubber tree. According to Napper, disease on a new clearing rises to a maximum between the second and third years after burning-off and then drops to a comparatively low figure.

However, Napper's findings have met with a certain amount of criticism by de Jong,⁷ who considers that Napper's method of estimating the status of the disease is open to question. De Jong found *Fomes lignosus* universally present in decayed root systems of all rubber trees up to 22 years on the H.A.P.M. estates in east Sumatra: it appears that the fungus is only weakly parasitic to *Hevea brasiliensis* and the presence of mycelium on the root system by no means augurs the subsequent death of the tree.

A great deal of confusion has persisted with regard to termites on rubber estates; it was formerly supposed that certain species known to be pests on plantations constructed termitaria in decaying tree stumps or built mounds just under the surface of the soil and, from these bases, made

attacks periodically on nearby rubber trees. It is now clear that *Coptotermes curvignathus* is the species which so frequently attacks young rubber with such disastrous results. It has already been pointed out that this termite constructs its termitarium deep underground and its complete eradication is difficult, if not impossible: the termites living in decaying timber and mounds have little or no interest in *Hevea brasiliensis*.

From the above consideration of the question of the advisability of burning cleared land, it will be seen that, in general, the practice has no special points to commend it. In fact, of the reasons in favour of the procedure given by Milne (page 108), (*d*) is not valid, and (*b*) and (*f*) hardly so, in equatorial regions. As regards (*a*), burning has the advantage of making certain nutrient minerals immediately available to the crop following, but in this connection the time of planting after burning may be of some significance. It is almost certain that losses of humus and nitrogen from the soil as a result of burning, (*c*) and (*e*), are inappreciable, as stated by Milne.

Of course, a question of this nature cannot be decided entirely on theoretical grounds for such matters as the crop following and clearing costs must be considered. In some countries with certain crops, for example, the cultivation of sugar cane in Trinidad and the Hawaiian Islands, planting is preceded by ploughing and, under these circumstances, burning of plant debris is essential.

LEGUMINOUS COVER PLANTS

In the early days of rubber cultivation it was customary to plant a "catch crop" between the rows of rubber trees; usually coffee was grown, but mainly as a result of difficulties with pests and diseases, this policy was abandoned in favour of one of "clean-weeding." In spite of obvious drawbacks the practice of clean-weeding had powerful advocates and for a long period in planting circles in the Malay Peninsula it was regarded as the only correct procedure. In these unenlightened times rubber estates were denuded of all

vegetation save rubber trees, but in the course of time, the evil consequences of the method became apparent, when plantations were left with hard-baked, impoverished soils and, often, on hillsides, the whole of the top-soil disappeared as a result of rainfall erosion. The failure of clean-weeding caused a reversion in planting policy and cover plants were now grown, primarily with a view to protecting the soil against erosion. The efficiency of covers as soil retainers is now undisputed, and Belgrave has shown that, in Malaya, no significant diminution in soil moisture content occurs in the presence of covers.⁸ The activity of nitrogen-fixing bacteria associated with the root nodules of leguminous plants was well known and it was suggested, quite reasonably, that low-growing species of Leguminosae might be employed advantageously as covers as they might do much towards reconditioning the soil on old rubber plantations.

As far as the Malay Peninsula was concerned the selection of a suitable legume species was not easy, as the cover was required to grow profusely on newly-cleared forest soil, exposed to the full glare of the sun, and then to continue to thrive under the shade of mature rubber trees. The ideal leguminous cover plant for rubber plantations in Malaya has not been found, although the problem has been largely solved in the Large Sunda Islands.

From first principles it would not have been anticipated that introduction of species of Leguminosae into the Malay Peninsula from the Sunda Islands would have been an unqualified success. It has been pointed out that in times not very remote the Large Sunda Islands, together with the present Malay Peninsula, formed a unified land mass and so shared a common flora and fauna (page 3). There is no reason for believing that the life of any particular species of plant or animal is infinite: on the contrary, it seems evident that the life of any plant species can be represented by a "life curve" in which an increasing population is followed by a decline and then by extinction (page 63). It is a fact that certain species of Leguminosae occur to-day in the Sunda Islands which have not yet been found in Malaya,

and the explanation of this absence from the Peninsula may be either that:

- (a) the plant formerly occurred in Malaya but has since died out naturally, or that
- (b) the plant never became established in the Peninsula, possibly because climatic or soil conditions were unsuitable.

In either circumstance, no strong case can be made out for introducing leguminous plants into Malaya from the Sunda Islands. In point of fact, the policy of bringing cover plants to Malaya from Borneo and Java has proved to be a failure, and probably a more costly one than is generally realized. On a few plantations some covers have done well, but there is little doubt that the policy in favour of employing leguminous covers is being abandoned as a general practice.

In Malaysia very few leguminous plants of low habit are to be found growing in the shade of the primeval forest: it has been indicated already (page 91) that apparently nodule-bearing legumes grow where they are most needed, that is, in open sunny situations, so there is little hope of finding in Malaya or Malaysia a leguminous plant suitable for the shade of rubber estates in the Peninsula. It is possible, but hardly probable, that such plants may be found in equatorial Africa or tropical America and, if so, their introduction into the East Indies may be attended with some measure of success.

The family Leguminosae is divided into three subfamilies: Mimosaceae (including *Mimosa*, *Acacia*, etc.), Caesalpiniaceae (comprising *Cassia*, *Caesalpinia*, etc.) and Papilioniceae. The last-named subfamily includes all the common American and European genera, such as *Lupinus*, *Pisum*, *Trifolium*, *Wistaria*, *Ulex*, *Cytisus* and *Genista*, and almost all members are known to possess root nodules. Considerably less is known concerning the formation of root nodules with the remaining two subfamilies: no nodules have been found on the roots of many species of *Cassia* and *Caesalpinia*, but nodule-formation appears to be the rule



FOUR YEAR OLD RUBBER WITH A COVER OF
CALAPOGONIUM MUCUNOIDES.

in the Mimosaceae (*Mimosa pudica*, the sensitive plant, has nodules⁹). Although never known to bear nodules, *Cassia tora* is used in the Hawaiian Islands as a green manuring crop with beneficial results: in this case it was considered possible that, although no nodules were formed, nitrogen-fixing bacteria might be present within the root tissue but it has been demonstrated that this is not so.¹⁰ It is evident that the mere selection of a legume as a cover plant does not ensure the presence of a nitrogen-fixing mechanism in the underlying soil.

Of the leguminous plants employed as covers in Malaysia the majority are creepers which often obtain a stranglehold on other low-growing vegetation, and so are useful in eliminating weeds. It is desirable that the covers should thrive under shade but few satisfy this requirement: most of the leguminous covers employed have deep and well-developed root systems, the presence of which doubtless serves a useful purpose in opening up the soil, which may have become closely-packed on old estates where the movements of coolies have not been restricted to paths.

The more important cover plants in use in the Malay Peninsula at present are:—

(a) CREEPERS

Calapogonium mucunoides: useful with young rubber but dies out under shade. A native of tropical America, it was found growing wild on the east coast of Sumatra and in Java some years ago, and was introduced into the Malay Peninsula about 1924.

Indigofera endecaphylla: used with young rubber but apt to die back in dry weather, and of little use under shade. Native to South India at an altitude of 3000 feet.

Centrosema pubescens: usually grows well in open situations and is not easily established under shade; nevertheless, it is reported as being able to continue to grow under shade if well established with young rubber. With this and the following species, the leaves close during the brightest parts of the day.

Centrosema plumieri: can grow well in open situations but is less satisfactory than *C. pubescens*. The *Centrosema* species are native to South America, but *C. pubescens* was found wild in Java in 1921.

Dolichos hosei (= *Vigna oligosperma*): the "Sarawak bean" often does well under heavy shade and is the leguminous cover which has grown best under the shade of mature rubber in the Malay Peninsula. The root system is shallower than usual with most plants of this group. *D. hosei* occurs wild in the Large Sunda Islands but appears to have been absent from Malaya until introduced from Borneo. It was first employed as a cover on rubber plantations in Sarawak, and it was formerly believed that the species was confined to Borneo: later, it was discovered that *Vigna oligosperma* from Java and Sumatra was identical with *D. hosei*.

Peuraria phaseoloides (= *P. javanica*): can be used under shade and prefers heavy soil. It is indigenous to Malaysia, being found growing over low shrubs in secondary associations on the plains.

Mimosa invisa: formerly enjoyed a measure of popularity but has a decided disadvantage in the fact that it harbours various species of insects.

(b) SHRUBS

Crotalaria anagyroides: a tall shrub which can attain a height of some twelve to fourteen feet and usually covered profusely with yellow flowers. It grows well in open situations and can survive dry periods; in Malaysia it grows at altitudes up to 5000 feet but has a tendency to die back after two years. The root system is known definitely to have nodules. Native to tropical America.

Several other species of *Crotalaria* are cultivated in Malaysia but *C. anagyroides* is most generally employed.

Tephrosia candida: can thrive under light shade although it prefers open situations. In Sumatra it is employed as a light shade and green manure for tea: it is native

to tropical Asia and occurs on the plains and at altitudes up to 5000 feet.

Leucaena glauca: appears to grow fairly well in open situations.

Non-leguminous plants employed as covers for rubber plantations are:—

Passiflora foetida (Family Passifloraceae): used extensively as a cover on new clearings as its creeping habit renders it particularly useful on hillsides. Although it grows well at the start, it disappears with the development of shade from the young rubber trees. Originally confined to tropical America, this species is now distributed throughout the equatorial belt.

Mikania scandens (Family Compositae): a native creeping plant, occurring on the forest edge at all elevations up to 4000 feet. It can thrive under light shade but cannot withstand drought.

Marremia vitifolia (Family Convolvulaceae): is a native plant which has recently been employed successfully as a cover under young rubber in Kedah.

The subject of leguminous cover plants in Malaya has been dealt with in a comprehensive manner by Bunting and Milsum.¹¹

With most leguminous cover plants cultivated in Malaya root nodules are usually present, although small in size and few in number, and it has been suggested repeatedly that nodule formation might be improved by inoculation with more vigorous strains of nodule-forming bacteria. A few experiments carried out by the writer with *Dolichos hosei* showed that inoculation alone produced no visible effect when small nodules were already present, but a temporary increase in the size and numbers of nodules followed the application of wood ash.

It has been mentioned already that, under natural conditions in Malaysia, a state of dynamic equilibrium exists in the soil under the shade of the primeval forest and it appears that leguminous plants play but a small part in maintaining this equilibrium. It may well be that the

nitrogen-fixing mechanism of these tropical legumes is unaccustomed to working under shade and so operates very inefficiently on plantations under mature rubber. If this is so there is no reason why leguminous rather than other plants should be employed as covers.

It has been emphasized repeatedly that, to obtain any benefit from the growth of covers, they must be turned into the soil at intervals; but recent work indicates that this view is, perhaps, hardly correct. The digging-in of cover plants on a rubber estate does not result in any *permanent* increase in the nitrogen content of the soil, in fact, rather is the reverse the case. It has been mentioned on page 99 that the nitrogen content of the soil is dependent on a number of climatic factors and cannot be permanently increased above a certain value, except by effecting alterations in these climatic factors. Addition of organic matter to the soil (e.g. digging-in of cover plants), under the same degree of shading as before, means that the added material is soon decomposed and completely disappears and any growing crop gains only a temporary benefit. The removal of growing cover, moreover, results in increased exposure of the soil to the sun so that the final value of the nitrogen content of the soil is probably lower than that which obtained before the cover was cut down. Under some conditions, of course, it is essential to cut the cover.

If the long view be taken, there can be little doubt that it is advisable to maintain rather than to dig in a growing cover, for it may be supposed that the soil nitrogen content will be slowly but surely increased by addition of dead leaves, etc. as the shade is increased. It has already been pointed out that a fall in the potential nitrogen level of the soil as a result of removal of shade appears to be accompanied by release of the excess nitrogen largely in the gaseous form, in which state it cannot be assimilated by growing vegetation.

NATURAL COVERS

EVILS OF CLEAN-WEEDING

Although the question of the use of covers for rubber plantations has been freely debated in the past, the practical

result has been that the pendulum of popular planting opinion has swung from one extreme to the other. The days of "catch crops" were characterized by efforts to extract the maximum profit from the soil in the minimum space of time, regardless of any consideration for the future, and the extremes to which the vogue of "clean-weeding" were carried were possibly attributable to experience of the evil effects resulting from the admittance of lalang. Although the disastrous consequences of clean-weeding are now only too evident, it is surprising that the practice was continued for so many years before being seriously questioned.

The deleterious effects of clean-weeding may be recapitulated:—

- (a) removal of shade results in a lowering of the potential nitrogen and organic matter content of the soil;
- (b) a hard-baked surface lacking an adequate moisture content is an evil which continually worsens as a result of the unrestricted movements of coolies, as has been pointed out by Haines;
- (c) the absence of surface vegetation and soil humic matter may mean that any nitrates are leached out by the intensive rainfall;
- (d) on hilly land considerable losses of soil occur as a result of erosion.

Once the consequences of a policy of clean-weeding were generally realized an attempt was made to meet the situation by the cultivation of some single plant species, usually one of the Leguminosae, as a cover. This idea of cultivation of covers in pure strain met with indifferent success in Malaya, although promising results were often obtained in Sumatra and Java. On the older plantations in the Malay Peninsula, where the top-soil had been non-existent for decades, attempts to cultivate leguminous covers usually proved a dismal failure.

THE BIRKEMOSE SYSTEM

It appears that the so-called "forestry system" was first successfully demonstrated by Mr. F. Birkemose in Pahang,

and on the particular estate the method proved to be such a striking success that there followed a desire on the part of Malayan planters to see how far the system was of general applicability.

When the experiment was started on the Pahang plantation the clay soil had a hard-baked surface, which was generally bare but carried a cover of stag-horn moss (*Lycomodium cernuum*) in some places. The soil was probably quite acid, and it is safe to say that microbiological life must have been at a minimum. In the beginning of the experiment any weeds which could gain a footing under the inauspicious circumstances and any rubber seedlings which germinated were given every encouragement, although an exception was made in the case ofalang grass which was rigorously excluded. At intervals the weeds were pulled up, or slashed down, and left to decay on the surface of the soil and, where considered necessary, the acidity of the soil was reduced by a light application of lime. In the course of time, as soil conditions became more kindly, further weed species appeared and gradually humus formation was set up and conditions became favourable for the normal microbiological processes of the soil to become operative again. Once a humus layer was obtained progress was more rapid, and a certain amount of selection could be exercised with regard to the species of plants allowed to obtain a footing, but weeds with a large and matted root system were excluded. Attention was paid to the conditions of light and shade, and subsequently earthworms were introduced and they increased rapidly. The soil containing an abundance of earthworms was generally friable, well-aerated and comparatively rich in humic matter. As the plants themselves are good indicators of soil conditions, once the normal cycle has been restored it can be maintained. This, in brief, is the Birkemose system employed in Pahang and there can be little doubt that its successful demonstration will prove to be a landmark in planting history in the Malay Peninsula.

In many respects the scheme is revolutionary and, naturally enough, has come in for some severe criticism: the subject



STAG-HORN MOSS (*LYCOPodium CERNUM*)

has been given a preliminary examination by the Rubber Research Institute of Malaya¹² and it is of sufficient interest to merit detailed examination here. Some very obvious advantages of the system are immediately evident. The natural habitat of *Hevea brasiliensis* is the humid forest of tropical South America and a procedure which has for its object the maintenance of conditions approaching those of the natural habitat of the tree is clearly to be encouraged; the establishment of a natural cover at a desired level is a first essential.

The restoration of a cycle entailing growth and decay of vegetation will ensure continual addition of organic matter to the soil, the growth of a light cover will result in the surface of the soil being adequately but not too densely shaded from the sun, and the soil will lose its hard-baked appearance and retain moisture and mineral salts. It has been pointed out already that in regions such as Malaysia, where the rainfall always exceeds the evaporation, there is a continual loss of soluble material downwards through the soil. If these water-soluble substances are retained in growing vegetation at the surface, although temporarily removed from circulation, they are lost to the main crop only for a time.

In addition to increased humic matter and moisture and the return of normal microbiological activity in the soil, there is a further important consequence of the "forestry" system which is that, as a result of increased shading of the soil surface, the potential organic matter content will be raised. Conditions will then be such that any extra nitrogen added to the soil will be retained in the normal cycle until the nitrogen content of the soil reaches the maximum value possible under the conditions of temperature and insolation which obtain. This point is of considerable importance, for it corresponds to an increase in capital of which the interest will be available for use by the cultivated crop.

Much research work remains to be carried out regarding the plant associations which appear under the conditions described. The term "natural covers," which is used so frequently in discussions on the Birkemose system, is not,

perhaps, a very happy one as many of the plants which are among the first to appear on old clean-weeded areas are introduced species and not indigenous to Malaysia (see Table IV).

Some experiments have been carried out in Malaya with bamboo as a cover for rubber¹³ and the idea merits further investigation, but it is possible that the dense litter thrown off by bamboo does not make for ideal soil conditions. The use of bamboo in pure stand, however, must not be confounded with the Birkemose system, the essential feature of which is to encourage the growth of a natural plant association. Bamboo has been successfully employed as a means of eradicating stag-horn moss in the Hawaiian Islands.¹⁴

DEFECTS OF THE SYSTEM

Two serious criticisms have been levelled at the "natural cover" system: one is on account of the possibility of increased disease to the rubber trees and the second is concerned with disease to human beings. The first may not be serious but it may well be that the system will stand or fall on the second count.

It is considered in some quarters that the "forestry" conditions described will encourage the growth and spread of pathogenic fungi. One of the features of the system is that old or diseased trees are cut off level with the ground and the root system is allowed to decay *in situ*: it has been pointed out that such a procedure may result in serious cumulative effects. The plant pathologist is within his rights in not minimizing the danger from this source, but it would have to be very grave to merit condemnation of the method without further investigation. Taking a broad view of the question, it is quite possible that disease will decrease rather than increase under the Birkemose method. It has been pointed out already (page 68) that, in general, the outbreak of an epidemic of any nature follows the bacterial growth curve, and it may be that the occurrence of epidemics is suggestive of artificial conditions. It is hardly probable now that any of the well known fungal



RUBBER WITH A MIXED NATURAL COVER.

diseases of the rubber tree would break out with greatly increased virulence: in fact, with a reversion to more natural conditions it would be anticipated that anything in the nature of epidemics would tend to disappear and that the growth curve for fungal diseases would tend rather to follow a straight line than to exhibit a number of crests and troughs corresponding to rises and falls in the population of disease-bearing organisms. That is to say, a certain amount of disease will be present always as a normal factor and as such it must be accepted. In mixed forests it is surely unusual for all the trees of any one species to die as a consequence of the appearance of a fungal epidemic.

Another point which must not be overlooked with regard to the question of natural covers and disease is that under the new system different soil conditions must be envisaged and it may be that pathogenic fungi will prove to be less resistant in less acid soils. De Jong could find no direct relationship between the incidence of *Fomes lignosus* on rubber trees and the reaction of the soil but, otherwise, little or no work appears to have been carried out on the relation between the pH of the Malaysian soils and the incidence of fungus diseases.⁷ All things considered, however, it would appear that, as a condition of equilibrium in the natural cycle on an estate is approached, there will be less likelihood of any one species of plant or animal increasing prodigiously at the expense of others.

The second objection that forestry methods may make for conditions inimical to human life is a much more serious one. It must be conceded that if natural growth is allowed to attain any dimensions it will harbour a population of wild life which will include small mammals, and this being so, the danger to humans from Japanese river fever and tropical typhus may be very real. In both these infections rats act as reservoirs and the disease is transmitted to man by mites. It has been submitted that the forestry method will encourage rodents and other small mammals able to carry these diseases by affording them protection, and it is known already that Japanese river fever and tropical typhus are often associated with the presence of cover plants and forest

growths. This suggests that a cover of a shrubby nature is preferable to one which covers the ground.

It is perhaps hardly necessary to suggest that a dense, uncontrolled cover of secondary growth may constitute a serious danger to a labour force if the possibility of lurking tigers is ever present.

From the standpoint of the agriculturalist, the Birkemose system has much to commend it, and it is to be hoped that it will not be condemned at the outset by unfair or prejudiced criticism; nevertheless, the question of disease both to the rubber tree and to human beings is an important aspect of the matter which requires thorough investigation.

THE EFFECT OF FERTILIZERS ON THE SOIL

Fertilizers are added to the soil with the primary object of supplying additional nutrient material to a growing crop, but their presence may prove to be advantageous in three ways:—

- (a) by supplying plant nutrient;
- (b) by interaction with substances already present resulting in the appearance of a third compound;
- (c) by altering the physical condition of the soil in certain respects.

It would appear that the most usual result is that described under (a), but here two cases have to be differentiated. Certain inorganic substances, such as nitrates and ammonium salts, are assimilated directly by the root system of the growing plant, but other compounds, such as urea, cannot be utilized by the plant until a certain amount of decomposition has been effected by microbiological or chemical means. It is only within the last few years that it has been established beyond question that ammonium salts can be assimilated as such by plants; formerly it was believed that nitrogen present in ammonium salts could be absorbed by growing vegetation only after oxidation to nitrate.

As an instance of the interaction of a mineral salt employed as a fertilizer with a substance already present in the soil

it may be mentioned that the addition of a potassium salt to certain soils is followed by release of adsorbed calcium, so that a supply of this latter element is rendered available to the plant. Fertilizers may affect the physical condition of the soil in a number of ways; addition of alkali salts to a clay soil renders it "sticky" and certain salts are not without effect on the pH value of the soil, either immediately or subsequently. Very little lime is required, however, economically to counteract the effect of ammonium salts in lowering the pH of the soil.¹⁵

Almost invariably manuring is carried out with a strictly commercial end in view, so that the subject has always to be considered from an economic standpoint. Although the yield of a crop may be increased by application of a fertilizer to the soil, it is evident that it cannot be augmented beyond a certain maximum: in fact, owing to the toxicity of many salts in high concentration, addition of excessive amounts of fertilizer may have a deleterious effect. In general, manuring is most successful when it is confined to the addition of certain substances known to be lacking from the soil under examination: thus in many Malayan soils the phosphate content becomes a limiting factor in crop production so that application of a dressing of superphosphate has often a marked effect on crop yields. The mere addition to the soil of materials removed in the crop, however, is not sufficient to ensure maintenance of a high measure of fertility.

In the presence of excess of nitrogenous manures the leaves of plants become large and dark green in colour and are particularly prone to attack by insect pests; in the absence of available nitrogen, growth is stunted and the leaves assume a yellowish colour. Starvation of potassium is characterized by the leaves yellowing at the tip and by physiological derangement: to a certain extent potassium acts as a corrective when excessive amounts of nitrogen are present, and it is well known that the full effect of either nitrogenous or potassium fertilizers is apparent only when the supply of the other is adequate. The lack of sufficient supplies of phosphate is associated with a stunted root

system, while the ripening of seed and fruit is hastened by addition of phosphate.¹⁶

MANURING OF RUBBER

With regard to the application of fertilizers to annual crops in the tropics it is possible that the governing principles do not differ widely from those in temperate regions. For example, if lack of phosphate were found to be the limiting factor in crop production then, other conditions being normal, application of superphosphate in suitable quantity should result in the production of an increased yield. Nevertheless, in sun-baked tropical soils on old plantations where humic matter is non-existent, any fertilizers depending on biological agency to render them available to plants may be lost by leaching before being brought to a condition in which they can be assimilated by the growing crop.

It is on annual crops that manuring is most likely to be practised extensively and in this case the success or failure of the procedure is soon evident. The question of manuring perennial crops such as rubber and coconuts is more complicated. Nitrogenous fertilizers are most frequently used and the situation here merits detailed consideration.

From the discussion in Chapter VIII, it is apparent that the nitrogen content of the soil depends primarily on the mean annual values of the insolation, temperature and humidity. As far as Malaysia is concerned, it appears that insolation is the most important of these climatic factors and, if the amount of solar radiation reaching the soil be increased by any means, loss of nitrogen ensues until a new and lower level is reached.

Speaking in general terms then, it seems safe to say that, in the soils under consideration, the nitrogen content varies inversely with the amount of solar radiation received and it is evident that effective shading must be a prelude to any efforts to raise the nitrogen status. In the absence of such shading, any nitrogen added to the soil in excess of that determined by the relationship just mentioned will be lost as speedily as the mechanism operating will permit.

There is abundant evidence to show that no permanent

increase in the nitrogen status of Malaysian soils can follow the application of nitrogenous fertilizers, unless conditions are otherwise favourable for the soil to accumulate nitrogen. According to the views just advanced, addition of nitrogenous material, such as urea or sulphate of ammonia, to the soil in exposed situations must be followed by losses of nitrogen (as elementary nitrogen, ammonium salts and nitrates) until the nitrogen content of the soil has fallen to its former level. It is true, however, that in spite of these losses growing vegetation will derive some benefit as a result of the presence of increased amounts of ammonium and nitrate ions in the soil solution, but the proportion of the fertilizer actually utilized by the plant may be surprisingly low.

Doubtless, these losses are not so rapid when nitrogen compounds are added to soil under the shade of mature rubber trees, but a difficulty here is that, on old plantations, the soil is so impoverished of organic matter that, in spite of increasing shade, the biological mechanism for making additions of nitrogen to the soil is absent and so the nitrogen content of the soil remains at a low level. On the other hand, although this application of fertilizers to *Hevea* may not result in any permanent increase in the nitrogen status, the added material will remain in the soil for a longer period and so give the roots of the trees a chance of utilizing some proportion of the extra nutrients present.

The question of the most satisfactory method of adding fertilizers to perennial crops in the humid tropics cannot be regarded as settled for, while the foregoing discussion suggests that it would be advisable to apply the fertilizer in a number of small applications, other considerations point to there being a minimum dose below which the manure is without effect.

Interesting results with rubber on the east coast of Sumatra have been reported by Grantham, who obtained responses to fertilizer treatment only on estates on "white" alluvial soil, where the soil is known to be poor in plant food material, and where rubber begins to decline rapidly when some five or six years old. On the other hand, prolonged

experiments have shown that certain "red" volcanic soils, exhibiting no initial response, began to give economic returns for manuring after 15 years, at which age deterioration normally sets in on this type of soil.¹⁷ Results obtained with rubber in Java have been much less spectacular and the improvement slower.¹⁸

In the Malay Peninsula, results have been almost uniformly disappointing and, in general, only with very poor and backward rubber is there any noticeable response to treatment with fertilizers. As Haines has pointed out, the amount of plant nutrient material removed annually in the latex is almost inappreciable, so that there need be no inevitability about approaching soil exhaustion such as occurs with annual crops.¹⁹ Nevertheless, as far as nitrogen is concerned, the present procedure as regards felling, clearing and planting is such that the eventual approach of soil exhaustion is assured, although it may be long delayed. And when this period of sterility does appear it is not to be expected that a dose or two of nitrogenous fertilizer will restore the *status quo*! At the risk of being tedious, it may be as well to emphasize that, once equilibrium has been attained, no amount of fertilizer treatment can permanently raise the nitrogen content of the soil—unless shading is increased and conditions are such that a return of normal biological processes is possible.

GARDEN SOILS

It is the usual experience of residents in humid tropical regions to find that addition of some kind of fertilizer, such as bullock manure, to the garden soil is essential every two or three months, if even moderate results are to be obtained with flower or vegetable cultivation. Unfortunately it is only too well known that the disappearance of this added manure is very rapid. From the discussion in Chapter VIII it is evident that these facts admit of a ready explanation: it has been pointed out that

- (a) the nitrogen and organic matter content of the soil varies inversely with the insolation and temperature, and



TAPPING A RUBBER TREE. THIS PLANTATION HAS BEEN CLEAN-WEEDED AND SILT PITS HAVE BEEN EMPLOYED IN ATTEMPTS TO CONSERVE THE EXPOSED TOP-SOIL FROM RAINFALL EROSION.

- (b) at temperatures above 25° C. humus decomposition proceeds at a greater rate than its formation.

The mean temperature of the soil in gardens on the plains is above 25° C. and it is clear, therefore, that in such soils there can be no accumulation of humic matter and, moreover, the nitrogen and organic matter content of the soil will readjust itself so that it remains at a low level. Repeated replenishment of soil nitrogen by artificial methods is a costly and unsatisfactory proceeding, but it is the only practical method of ensuring a temporary restoration of soil fertility under the circumstances described. It is essential to keep the soil shaded if humic matter is to be retained and, although it is not practicable to have a garden entirely under shade, a certain amount of soil conservation can be effected by retaining shade trees and encouraging suitable shrubs.

Fagraea fragrans (Malay "Tembusa") is a suitable shrub for waste patches in gardens in Malaya, for it grows rapidly on poor soil and produces shade conditions which make control of *Mimosa pudica* and lalang an easy matter: a drawback to *F. fragrans* is that it seems to have a fatal attraction for the tree ant or "kerengga" (*Oecophylla smaragdina*) and usually harbours an inordinate number of nests of this pest.

SUMMARY

The practical aspects of such matters as burning of cleared land, leguminous and natural covers and the employment of fertilizers are considered in the light of the views developed in the earlier chapters of the book.

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APPENDIX

I. STANDARD METHODS EMPLOYED FOR THE EXAMINATION OF SOILS

Mechanical analysis.

In the method of mechanical analysis now generally followed by British chemists the following classes are distinguished¹:

particle size above 2 mm. in diameter:	<i>gravel</i>
particle size between 2 mm. and 0.2 mm.:	<i>coarse sand</i>
particle size between 0.2 mm. and 0.02 mm.:	<i>fine sand</i>
particle size between 0.02 mm. and 0.002 mm.:	<i>silt</i>
particle size below 0.002 mm. in diameter:	<i>clay.</i>

In the Netherlands Indies, the soil fractions are divided somewhat differently: *gravel* particles are above 2 mm. in diameter, *sand* particles between 2 mm. and 0.05 mm., *silt* particles between 0.05 mm. and 0.005 mm. and *clay* particles below 0.005 mm. in diameter.

Soil moisture.

The soil moisture is estimated by weighing out 10 grams of soil in a weighing bottle and estimating the loss in weight, after drying to a constant weight in an oven at 105° C. Usually twenty-four hours will suffice to give a constant weight.

Loss on ignition.

The loss on ignition is used as a rough method of estimating the organic matter present in soils, but if calcium carbonate is present there is a loss of carbon dioxide due to the decomposition of this compound. The material is ignited to a constant weight in a crucible and the loss in weight taken as the organic matter. When calcium carbonate is present the ignited material is moistened with ammonium carbonate solution and heated gently, when calcium carbonate is re-formed, and the loss in weight is due only to organic matter and "combined water."²

Soil reaction.

The soil reaction can be determined roughly by colorimetric means, e.g. by use of the B.D.H. soil indicator and "Sofnol,"

but the results obtained are without precision. The quinhydrone electrode method³ is of general applicability at pH values below 8: in presence of manganese, however, the results are high⁴ and more accurate values are obtained with the hydrogen electrode.⁵

Total nitrogen.

It is customary to determine the total nitrogen present in soil by a modification of the Kjeldahl method. The air-dry soil is ground to pass through a 1 mm. sieve and then 20 grams are weighed into a Kjeldahl flask, followed by 50 ml. of water. After standing for about half-an-hour, 30 ml. of concentrated sulphuric acid, 10 grams of potassium or anhydrous sodium sulphate and 1 gram of copper sulphate are added. On completion of the digestion process, which takes about 5 hours, the liquid is poured into a distillation flask containing distilled water and, after addition of excess of 50 *per cent.* sodium hydroxide, the ammonia present is distilled into standard sulphuric acid. The excess of acid is determined by titration with sodium hydroxide, in presence of methyl red as indicator.

The estimations should be carried out in quadruplicate, but it is more satisfactory to make five or six parallel determinations.

Estimation of ammonia in soil.⁶

To 100 grams of fresh soil (not more than 50 grams in the case of peat) in a bottle are added 100 ml. of 2 *N* potassium chloride solution, sufficient hydrochloric acid to give the suspension a reaction of pH 1,⁷ and water sufficient to make the volume of the extraction medium up to 200 ml. After addition of a few drops of toluene,⁸ the bottle is closed with a tightly-fitting rubber bung and shaken in a shaking machine for 1 hour.

The contents of the bottle are then transferred to a large distillation flask to which are added 200 ml. of distilled water, a fragment or two of pumice and 4 grams of magnesia. The neck of the distilling flask is fitted with an ammonia trap, and the contents of the flask are distilled into a receiving flask containing a known volume of approximately 0.075 *N* sulphuric acid. When about 200 ml. of liquid have passed over, the receiving flask is removed, the contents are boiled for about 20 minutes to drive off carbon dioxide, and then titrated with 0.075 *N* sodium hydroxide, using methyl red as indicator.

The whole analysis should be carried out in duplicate and a control analysis should be made in which 100 ml. of the extraction

medium are made up to 300 ml. with distilled water and distilled with 4 grams of magnesia.

The moisture content of the soil must be estimated in a further sample and allowed for in calculating the ammonia-nitrogen present. In the case of soils rich in calcium carbonate, smaller samples must be taken and stronger hydrochloric acid employed.

Estimation of nitrite and nitrate.

The nitrite- and nitrate-nitrogen can be determined in the soil sample used for the estimation of ammonia. After distillation of the ammonia a further 200 ml. of distilled water are added, together with 3 grams of Devarda's alloy and 1 ml. of ethyl alcohol, and the contents of the flask are distilled into 0.075 *N.* sulphuric acid as before. Any nitrite and nitrate present is reduced to ammonia by the alloy and the acid neutralized is estimated by titration with sodium hydroxide as before.

In soils of the humid tropics nitrites are rarely found so the ammonia found after reduction by Devarda's alloy usually represents nitrate-nitrogen only. If nitrite is present (test with the Griess reagent⁹) it must be estimated in a separate sample.

Estimation of nitrite in soil.

About 20 grams of fresh soil are taken and extracted with 100 ml. of distilled water. After filtration, 25 ml. of solution are taken and made up to a definite volume, say 50 or 100 ml., after addition of 2 ml. of each of the Griess reagents,⁹ and the colour produced is compared in a colorimeter with that obtained from a standard nitrite solution containing the same quantity of the Griess reagent. In this estimation the colours should be compared after a definite time has elapsed since preparation of the solutions, say 8 or 10 minutes.

In the presence of clay, the aqueous filtrate obtained after extraction of the soil may be cloudy and in such a case the procedure must be modified; to a known weight of fresh soil is added approximately the same volume of a 0.5 *per cent.* solution of aluminium sulphate and the mixture is shaken for ten minutes. Then about 1 gram of calcium hydroxide is added and after further shaking the mixture is left to stand; the soil settles quickly, and the clear extract can be removed by filtration and used for the estimation of nitrite.¹⁰

Estimation of the numbers of soil micro-organisms.

The procedure described below was found to give satisfactory

results with soil samples in the Malay Peninsula. It must be noted that the method assumes that

- (a) each colony which develops on the plate represents a single organism;
- (b) every viable organism in the sample which falls on the plate forms a colony.

In practice neither condition is fulfilled.

Sampling. The composition of the soil is so variable that results based on a single sample are almost valueless. Sampling is best carried out by a set of metal tubes, two inches in diameter and some six or eight inches in length; for most experimental purposes sampling should be carried out to the same depth, which may conveniently be four or six inches. Accordingly a mark is filed four or six inches from one end of the tube, and, when sampling, the tube is driven into the ground until this file mark is flush with the surface. The practice of bulking three or four cores is indefensible on mathematical grounds, although no serious error is introduced when the concentration of micro-organisms does not differ widely from one sample to another. At least two samples should be taken.

It is a good plan to carry out the plating operations when the samples are of the same age; twenty-four hours after sampling is usually a convenient time, as it permits examination of samples taken at some distance from the laboratory.

Preparation of the plates. 2.5 grams of soil are weighed out (at this stage it is unnecessary to adopt any precautions against contamination by stray organisms) and added to 250 ml. of sterile water¹¹ contained in a 500 ml. flask. This flask, which previously had a wad of cotton wool in the neck, is now closed by a sterile rubber bung. If the soil has not been sieved, at this point it may be advisable to insert a sterile glass rod into the flask and grind any lumps of soil to powder. The flask is now shaken by hand so that an arc about 3 feet in length is described fifty times.

The flask contains 1 gram of soil per 100 ml. of liquid, and it will be necessary to make higher dilutions. Ten ml. are taken out by a sterile pipette and placed in a bottle containing 90 ml. of sterile water (or saline); the solution is sucked up and down the pipette once, then the bottle is closed by a sterile rubber bung and shaken by hand until complete admixture has taken

place. This results in a dilution of $1/1000$, which is usually sufficient in Malaya; nevertheless, in starting a series of plate counts it is well to make dilutions of $1/1000$, $1/10,000$ and $1/100,000$, and the higher dilutions can be omitted subsequently, if found to be unnecessary.

Finally, 1 ml. of the dilutions employed is taken in a sterile 1 ml. pipette and placed in a sterile petri dish, and this is followed by addition from a test-tube of 10 ml. of agar medium which has been melted in a water bath and then cooled to 42°C . At least four platings of each dilution of each sample should be made and, immediately after addition of the agar, the plate should be given a circular motion to ensure proper mixing of the soil solution and agar. The petri dishes are then set aside to cool and are inverted when solid and placed in an incubator. In Malaya the plates were incubated at laboratory temperature (26° – 29°C .) and the colonies counted after five days. If counting is delayed beyond this period it will be found that many of the plates are useless on account of being overgrown with fungal colonies.

The counting is carried out by inverting the petri dishes, ruling two diameters at right angles on the plate containing the agar, and counting the colonies in each quarter. The actual counting is carried out with a hand lens (magnification $\times 4$), and each colony is marked with an ink dot as counted. If the same lens is used throughout the investigation there is no need to subject the eyes to a severe strain in an endeavour to enumerate colonies not clearly visible with the lens.

From the foregoing it will be realized that all colonies should be counted unless it is specially desired to distinguish between fungi and bacteria. The total plate count recorded is that developing from 1 gram of moist or dry soil; if results are expressed on a dry basis the moisture content of the soil must be determined.

Sterilization of apparatus. If much bacteriological work is to be carried out it is advisable at the start to arrange the sterilization processes so that they are as automatic as possible.

The petri dishes may be sterilized by heating in an air-oven at 160°C . for two hours, and then wrapped in grease-proof paper, or a number may be placed in a proper metal petri dish-container and the whole sterilized in the autoclave between one and two atmospheres (120° to 130°C .) for thirty minutes. The rubber bungs may be placed in a large beaker of water, covered with

stiff paper, and sterilized in the autoclave. Pipettes are conveniently sterilized just before use in an instrument sterilizer and removed by means of forceps passed through the flame a few times immediately before use. The flasks and bottles containing water or saline are closed by a plug of cotton wool, over which is placed a covering of paper secured by an elastic band, and heated in the autoclave at 120° to 130° C. for half-an-hour. It is a great convenience if the pipettes employed are graduated right up to the tip.

The process of autoclaving results in a certain loss of water from the flasks and bottles, but this difficulty can be overcome by a simple preliminary experiment to determine the approximate loss of water from both the 250 and 90 ml. lots and adding the extra amount of liquid required before sterilization.

Thornton's agar count medium. Thornton's medium¹² is composed of the following constituents:

Dipotassium hydrogen phosphate	1.0 g.
Potassium nitrate	0.5 g.
Magnesium sulphate	0.2 g.
Calcium chloride	0.1 g.
Potassium chloride	0.1 g.
Sodium chloride	0.1 g.
Asparagine	0.5 g.
Ferric chloride	0.002 g.
Agar	15 g.
Distilled water	to 1 litre.

(*Note.* In equatorial regions it may be necessary to add more than 15 grams of agar to ensure solidification of the medium and the minimum quantity necessary is best found by trial.)

The salts are dissolved in water, then the agar is added, and the whole is melted in the steamer. The mixture is filtered through a thin layer of cotton wool in a Buchner funnel and 1 gram of mannitol is added to the filtrate. The reaction of the medium is adjusted to pH 7.3 with sodium hydroxide solution by means of brom-thymol-blue as indicator. The medium is tubed in 10 ml. lots and autoclaved at 120° C. for fifteen minutes.

Interpretation of the results of plate counts. The significance of the results can be accurately assessed only by submitting them to a statistical analysis.

Before starting an experiment, it is well to examine the variability of the soil by making plate counts on a large number

of samples taken simultaneously, and then to determine the error of the method by making a number of separate determinations on the same sample. In both cases the standard error of the determinations can be found and will be useful subsequently; in neither case should it exceed 20 *per cent*.

The *arithmetic mean* is found by dividing the sum of the colonies on all the parallel plates for a particular sample by the number of plates. Thus,

$$m = \frac{\Sigma a}{n},$$

where a is the number of colonies on a plate and n is the total number of plates.

The *geometric mean* is the arithmetic value which corresponds to the mean of the values of the logarithms.

The *standard error* is given by the formula:

$$\text{S.E.} = \sqrt{\frac{\Sigma(m-a)^2}{n(n-1)}},$$

where m is the arithmetic mean, a is the number of colonies on the plate, and n is the number of plates.

On the $P = 0.05$ level of significance, two values are significantly different from each other when the difference between them is greater than three times the standard error: that is to say, two values which were not significantly different could show a difference of three times the standard error by chance only once in twenty times.

If the frequency distribution of a number of platings of the same soil sample be plotted, a J-shaped curve is obtained, but if the logarithms of these values are so treated the usual bell-shaped curve, characteristic of a normally distributed population, is obtained. During the period between sampling and analysis the soil micro-organisms are passing through the phase of decline when the decrease in numbers is logarithmic, so that it seems safe to say that the geometric, and not the arithmetic, mean should be taken when averaging the results of a number of different samples. The mean value for a number of platings of the *same* sample should be averaged in the usual way from the actual values.¹³

In Fig. 10 are shown the distribution frequencies of the logarithms of the whole of the "bacterial counts" obtained by the writer for soils in the Malay Peninsula. The histogram is

characteristic of a normally distributed population, if some eight or nine high values (all taken during a period of "burning-off" on an area recently cleared of forest) be excepted. Excluding these "burning-off" samples, the mean value of the logarithms of the counts coincides with the mode of the curve. This

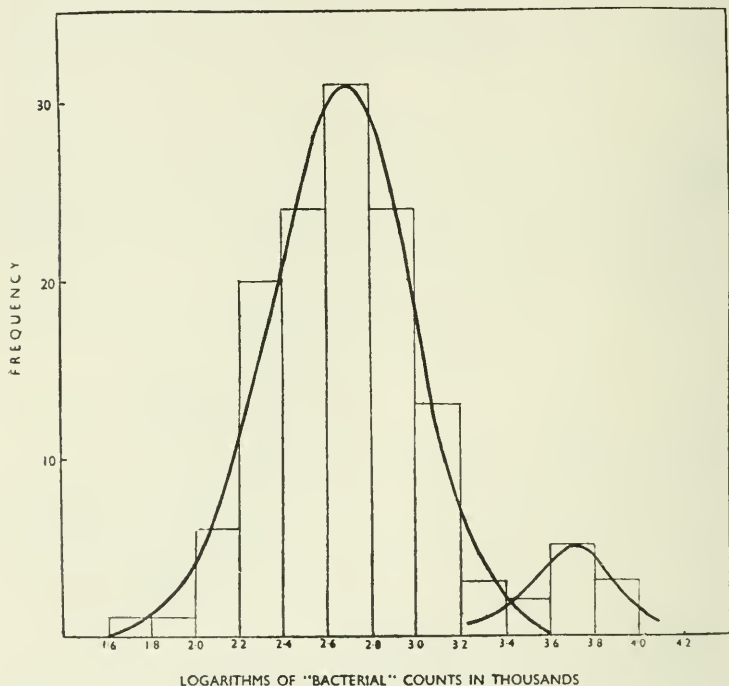


FIG. 10. THE DISTRIBUTION FREQUENCIES OF THE LOGARITHMS OF "BACTERIAL COUNTS" MADE IN MALAYA WITH SOIL UNDER FOREST, UNDER SECONDARY GROWTH, AND CLEAN-WEEDED AND EXPOSED TO THE SUN.

corresponds to a value of 500,000 micro-organisms per 1 gram of soil, while the mode of the curve for the samples taken during the "burning-off" period corresponds to a value of 5 million micro-organisms per 1 gram of soil.

II. CLASSIFICATION OF BACTERIA

Bergey's scheme of classification of bacteria is briefly appended in so far as commonly occurring soil bacteria are concerned.

CLASS SCHIZOMYCETES

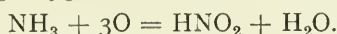
Order Eubacteriales

This order comprises all bacteria, except the Actinomyces and allied forms and the alga-like "higher bacteria." The cells occur as spheres or as straight or curved rods; they are motile or non-motile and some species possess endospores.

FAMILY NITROBACTEREAE

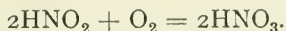
Cells usually rod-shaped and motile or non-motile; endospores not present. All are obligate aerobes, securing energy by the oxidation of carbon, hydrogen or nitrogen, or of simple compounds of these. Two tribes are recognized:

(a) Tribe Nitrobacterae, in which energy is secured by oxidation of simple compounds of carbon and nitrogen, e.g. alcohol, nitrites. This group contains some important and interesting forms. NITROSOMONAS [*europaea* Win.]¹⁴ effects the oxidation of ammonia to nitrous acid and is an important factor in soil fertility, particularly in temperate regions. It is sensitive to pH changes, growing best between pH 7.6 and 8.1; it cannot be cultivated in the laboratory in presence of more than small amounts of organic matter. The organism is strictly aerobic, requiring oxygen in accordance with the equation:



NITROCOCCUS [*nitrosus* (Mig.)] is a coccoid-like form of lesser importance which also effects the oxidation of ammonia to nitrous acid; it may prove to be identical with *Nitrosomonas*.

NITROBACTER [*winogradskyi* Buch.] is a rod-shaped, non-motile organism which brings about the oxidation of nitrous acid to nitric acid:



It works best at pH values ranging between 6.8 and 7.4; often it appears to be scarce or absent from soils, and it is probable that its importance in the nitrogen cycle in the soil is over-rated.

THIOBACILLUS [*thioparus* Beij.] is a small rod-like organism responsible for the oxidation of sulphur or simple sulphur compounds.

(b) Tribe Azotobacterae, containing nitrogen-fixing organisms. AZOTOBACTER [*chroococcum* Beij.] is a large obligate aerobe occurring as rods or cocci. In a medium deficient in nitrogen and in the presence of carbohydrates it can fix nitrogen

from the air. It is reported to work only in media with a pH value above 6.0, but it appears to be widely distributed in the cultivated soils of Malaysia. The sensitivity of *Azotobacter* to acidity and to the presence of phosphate has led to the use of this organism as a means of assessing soil fertility.¹⁵ It seems that *Azotobacter* cannot develop in the absence of iron compounds.

The species of RHIZOBIUM [*leguminosarum* Frk., better known as *radicicola* Beij.] are responsible for nodule formation on the roots of leguminous plants and are able to fix atmospheric nitrogen. It appears probable that nodule formation and nitrogen fixation occur largely where there is a deficiency in the nitrogen level. The species of *Rhizobium* are obligate aerobes, having a complicated life cycle; at one stage flagella are developed and the motile organisms are able to move rapidly through the soil. Entrance to a growing plant is effected through the unicellular root hairs.¹⁶

FAMILY COCCACEAE

Cells spherical and division takes place in one, two or three planes. Motility is rare and endospores are usually absent. The metabolism is complex, involving the utilization of amino acids and carbohydrates.

The Tribe Micrococceae comprises species which grow well on artificial media under aerobic conditions and many form pigments. The genus MICROCOCCUS [*luteus* (Schr.)] contains a large number of species, many of which are found in the soil; in some cases yellow pigments are produced while in the allied genus RHODOCOCCUS [*rhodochrous* Zopf] the pigment is a bright red.

FAMILY BACTERIACEAE

Rod-shaped organisms which may be motile or non-motile; endospores are absent and metabolism is complex.

(a) Tribe Chromobactereae is characterized by the production of pigment. SERRATIA [*marcescens* Bizio] comprises small aerobic organisms which produce red or pink pigments. The larger species of FLAVOBACTERIUM [*aquatilis* (Frkd.)] and CHROMOBACTERIUM [*violaceum* Bergon.] produce yellow- and violet-coloured pigments respectively. PSEUDOMONAS [*acrogena* (Schr.)] produces a water-soluble pigment of a green or blue hue.

(b) Tribe Protaminobacterieae contains the single genus PROTAMINOBACTER [*alboflavum* den Dooren de Jong], in which the species are able to attack substances containing amino groups.

(c) Tribe Cellulomonadeae, containing the single genus CELLULOMONAS [*biatotea* (Kell.)], is important in that its members effect the aerobic destruction of cellulose in the soil: these organisms may be motile or non-motile and chromogenic or non-chromogenic. Under very acid conditions in the soil (*pH* 4 or less), however, cellulose decomposition occurs largely as a result of the activities of fungi (*Trichoderma* and *Penicillium*).¹⁷

(d) Tribe Achromobacterieae contains the single genus ACHROMOBACTER [*liquefaciens* (Eisenb.)], which comprises rods which may be motile or non-motile and are rather variable in size and in cultural characters.

(e) The Tribe Erwineae consists of a number of plant pathogens.

FAMILY BACILLACEAE

Rods producing endospores. Only two genera have been separated.

BACILLUS [*subtilis* (Ehrenb.)] consists of a number of aerobic forms which are mostly saprophytes. The well known "Bacillus coli" is a species of *Escherichia* pertaining to the previous family.

CLOSTRIDIUM [*butyricum* Prazm.] comprises anaerobes and micro-aerophiles which are often parasitic. Many of the species are pathogenic and the well known *Cl. botulinum* v. Ermen. produces one of the most powerful toxins known. Several species of the genus occur in the soil and are able to fix atmospheric nitrogen; a few forms can effect the anaerobic destruction of cellulose.

Order Actinomycetales.

In this order the cells are usually elongated and frequently filamentous, with a decided tendency towards the development of branches. Endospores are not produced but *conidia* (i.e. reproductive cells) are found in some genera. The organisms are non-motile and usually aerobic; the metabolism is complex. Some species form mould-like colonies.

FAMILY ACTINOMYCETACEAE

Comprises a number of filamentous forms which are often branched and sometimes forming *mycelium* (i.e. a network of

thread-like hyphae); conidia are present in some species. It has been shown that the *Actinomyces* in the soil in India are present almost exclusively as conidia, and vegetative mycelia are found only when the organism is mixed with undecomposed plant remains.¹⁸

The genus *ACTINOMYCES* [*bovis* Harz] contains a large number of forms, but the specific identity of many of them is open to question.

FAMILY MYCOBACTERIACEAE

Straight or curved rods which are rarely filamentous: conidia absent.

The genus *MYCOBACTERIUM* [*tuberculosis* (Koch)] contains several aerobic species, mostly pathogenic to animals and of little importance in the soil. The species of *MYCOPLANA* [*dimorpha* Gray and Thornton] are able to decompose phenol: the recently described genera *CYTOPHAGA* [*hutchinsoni* Win.], *CELLVIBRIO* [*ochraceus* Win.] and *CELLFALCICULA* [*viridis* Win.] may prove to be important as they contain a number of soil organisms which decompose cellulose.

Order Chlamydobacteriales

FAMILY CHLAMYDOBACTERIACEAE

The alga-like "higher bacteria" usually occur as filaments consisting of a number of cells enclosed in a sheath. The species of *LEPTOTHRIX* [*ochracea* Kütz.] and *CRENOTHRIX* [*polyspora* Cohn] occur in iron-containing waters, and frequently the sheath is coloured dark reddish-brown on account of the deposition of ferric hydroxide.

III. CLASSIFICATION OF FUNGI

It is usual to divide the Fungi into the classes Phycomycetes and Eumycetes (comprising the sub-classes Ascomycetes and Basidiomycetes) and the Fungi Imperfecti. The characters of these groups are briefly outlined below.

CLASS PHYCOMYCETES

The two types of sexual reproduction found in the "algal" fungi form the basis for the differentiation of the two orders Zygomycetes and Oomycetes. In the first-named group, the sexual organs are similar and *zygospores* are formed by the conjugation of cells from different individuals; asexual reproduction

is effected by non-motile endospores. The Oomycetes are characterized by well-differentiated reproductive organs, a large female element uniting with a smaller male body to form an *oospore*. Asexual generation in the Oomycetes is effected by conidia and also by motile endospores termed *zoospores*.

Many of the best known soil fungi, such as *Mucor*, *Rhizopus* and *Zygorhynchus* of the family Mucorineae, pertain to the Zygomycetes, and of the few species parasitic on plants and insects, the house fly fungus, *Empusa muscae*, may be instanced.

Most of the Oomycetes are parasitic on plants, and some of the most destructive fungi known belong to this order. *Phytophthora infestans* is responsible for potato disease and *Plasmopara viticola* produces the "false mildew" on the leaves and fruit of the grape vine.

CLASS EUMYCETES

In the important sub-class ASCOMYCETES asexual multiplication takes place by means of conidia. When sexual generation occurs, conjugation of the sex elements results in the formation of an *ascus*, which is a club- or oval-shaped sporangium containing a definite number (usually eight) of *ascospores*. In few instances have the sexual methods of reproduction in the Ascomycetes been investigated.

This sub-class contains many important forms, among which may be mentioned *Aspergillus* (found on damp bread and vegetables), the blue-green mould *Penicillium*, the ergot-producing *Claviceps purpurea*, *Taphrina* (responsible for the formation of "witches' brooms") and the well known yeast fungi (Saccharomycetes).

In the sub-class BASIDIOMYCETES asexual reproduction occurs by conidia formation; the more or less distinctive conidiophore is termed a *basidium* and *basidiospores* are produced by a process of budding. Evidence of sexuality among the Basidiomycetes was lacking until quite recently when bisexuality was established in two members of the sub-class.¹⁹

*Fomes lignosus*²⁰ and *Gandoderma pseudoferreum*, which are responsible for root diseases on *Hevea brasiliensis*, pertain to this group, and the fructifications of the Hymenomycetes are known as toadstools.

FUNGI IMPERFECTI

As "Fungi Imperfecti" are grouped all forms not known to produce fruits characteristic of the other groups and, consequently, much diversity of form is shown. It is believed that

many conidial forms of the Ascomycetes are included here, and it is probable that further study of the group will reduce its numbers. Important soil genera pertaining to the division are *Oidium*, *Trichoderma* and *Fusarium*.

Many tropical plant pathogens belong to this group, among which may be mentioned *Oidium heveae*, causing secondary leaf fall in rubber trees, *Helminthosporium incurvatum*, which attacks the leaves of the coconut palm and *Fusarium cubense*, causing Panama disease of bananas.

IV. CONVERSION FACTORS

For conversion of degrees Fahrenheit to degrees Centigrade:

- (i) subtract 32 from the Fahrenheit value,
- (ii) multiply by 5,
- (iii) divide by 9.

For conversion of degrees Centigrade to degrees Fahrenheit:

- (i) multiply the Centigrade value by 9,
- (ii) divide by 5,
- (iii) add on 32.

For conversion of metres to feet:

multiply by 3·28.

For conversion of feet to centimetres:

multiply by 30·48.

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7. The amount of hydrochloric acid necessary to make the pH value 1 is found as follows: N acid is added from a burette until a drop of the suspension gives a clean blue colour with Congo red paper which does not alter on standing for five minutes; this brings the pH value to 2.0, and a further 20 ml. of N acid are then added.
8. It is doubtful if the addition of toluene has any significance.
9. For the Griess reagent two solutions are prepared:
 - (a) 10 g. of sulphanilic acid dissolved in 1000 ml. of 30 per cent. (by volume) acetic acid by heating on the water bath.
 - (b) 3 g. of α -naphthylamine boiled with 700 ml. of water for two minutes, then filtered and 300 ml. of glacial acetic acid added. The two solutions are kept separate and about 2 ml. of each are added to the solution to be tested. In the presence of nitrite a bright carmine colour is developed.
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